UNITED STATES DEPARTMENT OF AGRICULTURE
BULLETIN No. 957
Contribution from the Bureau of Plant Industry
WM. A. TAYLOR, Chief

Washington, D. C. PROFESSIONAL PAPER February 6, 1922

INVESTIGATIONS OF THE WHITE-PINE BLISTER RUST

By

PERLEY SPAULDING, Pathologist,
Office of Investigations in Forest Pathology

CONTENTS

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CONTENTS.

SCOPE OF THE INVESTIGATIONS.

In a previous publication (131)[1] the writer collected data on the more practical aspects of the white-pine blister rust, as presented in European literature.

Experience has shown that the white-pine blister rust has come to North America to stay and that most careful and searching investigations must be maintained to enable us to cope with it at all successfully. Investigations in Europe have been carried on in a desultory way for 35 years. In North America they were begun less than 15 years ago. Really intensive work has been in progress for only about 5 years. Considerable new experimental work has been done n Europe since the appearance of this earlier publication. At various imes since 1911 some of the more salient results of the investigation f *Cronartium ribicola* Fischer and the disease caused by it have been ublished (132 to 148, 180). During the years 1915 to 1919, inclusive, publication has fallen far behind the investigations.

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[1] The serial numbers in parentheses refer to "Literature cited" at the end of this bulletin.

No attempt has ever been made to collate and summarize the results of all the experimental work. The mass of information is so large and so scattered that it is nearly impossible for a single individual, even now, to learn what has been done. This condition is certain to become more and more acute as the extensive and intensive researches now under way progress. Various States are taking up work on this disease, and the multiplication of workers can only result in confusion and unnecessary duplication of work unless the ascertained data are arranged and made available for all. This bulletin aims to present the available information so that the gaps in our knowledge may be readily perceived and new investigations planned to the best advantage.

The work of the Office of Investigations in Forest Pathology has been conducted under the direction and advice of the writer by the following persons: In 1915, G. F. Gravatt and Dr. G. R. Lyman; in 1916, Dr. R. H. Colley, G. F. Gravatt, and Miss M. W. Taylor; in 1917, Dr. R. H. Colley, G. B. Posey, G. F. Gravatt, Rush P. Marshall, and Miss M. W. Taylor; in 1918, Drs. R. H. Colley, H. H. York, L. H. Pennington, L. O. Overholts, A. S. Rhoads, T. C. Merrill, W. H. Snell, D. M. Benedict, and Miss M. W. Taylor; in 1919, Drs. R. H. Colley, H. H. York, and L. H. Pennington, D. M. Benedict, J. E. Lodewick, W. H. Snell, P. R. Gast, Miss A. E. Rathbun, and Miss M. W. Taylor. Dr. G. G. Hedgcock made a comparative study of *Cronartium occidentale* and *C. ribicola* on Ribes on Block Island, R. I., in 1919.

The work of Dr. L. H. Pennington, D. M. Benedict, and J. E. Lodewick, in 1919, was maintained in formal cooperation with the New York State College of Forestry at Syracuse University.

The endeavor has been to show plainly in this bulletin who did each piece of work without entering into details to an objectionable extent.

The writer thanks the following people for unpublished data which have been placed at his disposal: Mr. W. A. McCubbin, formerly of Canada; Dr. Ed. Fischer, of Switzerland; Dr. A. B. Borthwick, of Scotland; Mr. A. D. Cotton, of Kew Gardens, England; Prof. L. Mangin, Museum of Natural History, Paris; Prof. F. Kølpin Ravn and Mr. J. Lind, of Denmark; Dr. L. O. Kunkel and Mr. W. Stuart Moir, of this country.

The writer and his collaborators are indebted for material for experimental use to the Arnold Arboretum of Harvard University; the Dominion of Canada Central Experimental Farms; the Park Board of Rochester, N. Y.; the Conservation Commission of the State of New York; the Office of Horticultural and Pomological Investigations and the Forest Service, of the United States Department of Agriculture. The Office of Blister-Rust Control has contributed data, especially toward that appearing in the chapter on control, Table V, and the list of Ribes species infected in the different States. Much difficulty has been encountered in getting satisfactory translations of articles published in the Japanese, Russian, Dutch, Swedish, Norwegian, and Danish languages. Dr. E. P. Meinecke has very kindly translated most of the Scandinavian and Danish articles. Mr. Rush P. Marshall and Miss M. W. Taylor, have aided in checking and collating the extensive data here presented.

In this bulletin the behavior of *Cronartium ribicola* is given with considerable detail. So far as is now known, it agrees essentially with the Uredinales in general in its life history and physiology. This is the first species of Cronartium to be very intensively investigated, and as a representative of this important group of forest-tree fungi, a detailed knowledge of its life history must form the basis for the institution of new methods of management of white-pine forests.

ORIGIN AND DISTRIBUTION OF CRONARTIUM RIBICOLA.

Some writers (76, 90) have believed that *Cronartium ribicola* went to Europe from America on *Ribes aureum,* that host being associated with it (but not exclusively) in the earlier discoveries of the disease in Europe. Magnus, who was of this opinion at first (90), seems to have completely rejected this theory and now believes that the disease came from western Siberia and the Swiss Alps, where it is supposed (26, 39, 40, 93, 130, 174) to have been endemic on *Pinus cembra.* In 1842 Klotsch issued in the exsiccatæ entitled "Herbarium vivum mycologicum, No. 490," a specimen labeled "Uredo ribicola" collected by Lasch at Driessen. Specimens have not been seen by the writer, and there is some uncertainty whether or not this is actually the uredinial stage of *Cronartium ribicola.* Sydow (155) gives it as a synonym of *C. ribicola,* but he is the only author known to the writer who does so.

Cronartium ribicola was first certainly found by Dietrich (27) in the Baltic provinces of Russia in 1854. He found it upon *Ribes nigrum, R. "rubrum,"* and *R. "palmatum,"* and also upon *Pinus strobus,* although at that time it was not known that the two forms were stages of a single fungus. So far as can be determined from scientific literature, it was not again noted until 1861 in Finland (81), 1865 in East Prussia (76), and 1869, when Eriksson (31) found it in Sweden on *Ribes nigrum,* and Hisinger (54) noted the first outbreak on pines in Finland. It had attacked *Pinus strobus* trees 30 years old and killed them. In 1883 Rostrup (115) reported an outbreak in Denmark on *Pinus strobus* trees 20 to 30 years old. It was evidently then generally spread over that country. Still later, Klebahn (62, 63) and Tubeuf (169) record it as generally distributed over

Germany, and soon it had spread over the northern countries of Europe (91, 92, 93). It seems to the writer that this was an instance of the introduction of a foreign disease into Europe and its destructive spread over most of that continent (39, 40). The fact that *Pinus strobus* had been grown extensively in Europe since its introduction there in 1705 (5), but was not known to have this disease until about 1855, in the light of our experience with this and other introduced plant diseases in North America, shows that this was a new disease which had reached Europe probably years before its discovery.

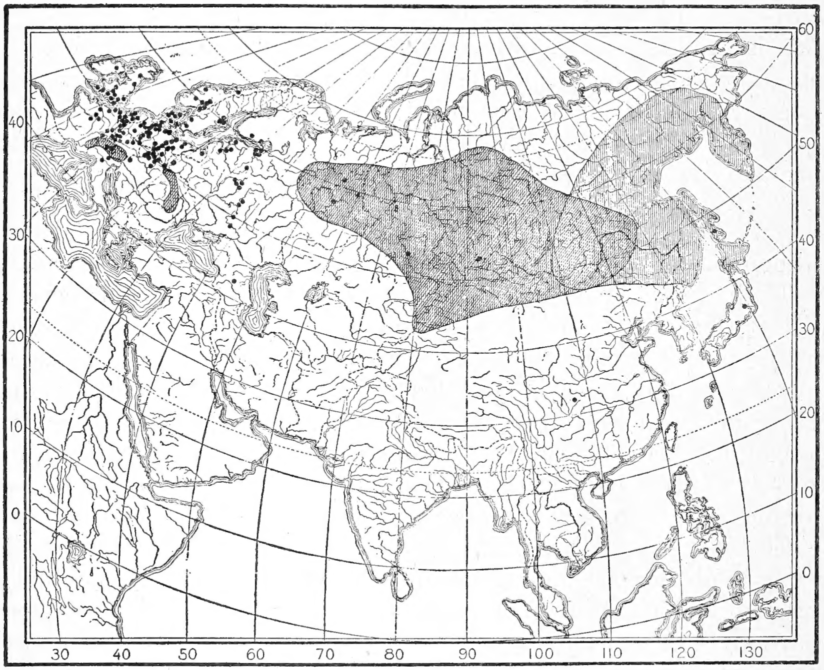

Fig. 1.—Outline map of the Old World, showing the approximate distribution of *Pinus cembra* (oblique hatching) and of its variety *pumila* (vertical hatching) together with the known distribution of *Cronartium ribicola* (black dots). Tree distribution furnished by the Forest Service, United States Department of Agriculture.

It is not certain that *Cronartium ribicola* is a native of the Swiss Alps (174). Schellenberg (123), in 1903, found *Cronartium ribicola* on a single 15-year branch of a tree of *Pinus cembra* about 200 years old in the Engadine Valley, Switzerland. He believed that the fungus was native there on this host. Yet this is the first known finding of the fungus on pine in that region. Ribes diseased with it were found there in 1895 (39, 123), showing it to be established in that locality then. It seems to the writer that the circumstances point plainly to the fungus having come into Switzerland some time previously, and that it is not endemic there; else it would have been found much earlier, and more of it would have been found since then. Fischer (40) found the disease in 1915 spreading into western and northern Switzerland from without.

It is generally supposed that *Pinus cembra* (26, 70, 93, 97, 98, 123) is the original pine host of this fungus. Figure 1 shows the distribution of *P. cembra* and its variety *pumila* in Europe and Asia. *Cronartium ribicola* is reported from Asia as follows: In 1879, from Bolschaja Inja River (131, 161); also from Tomsk and Minusinsk, Siberia (131). Quite recently it has been reported from Sakhalin Island and from Sapporo, Japan (156). Tulasne (175) in 1854 reported a Cronartium on Ribes, probably in India. Clinton has announced (13) the finding of *Cronartium ribicola* on dried herbarium specimens of Ribes collected by Wilson in the western part of the Province of Hupeh, China, in 1900.

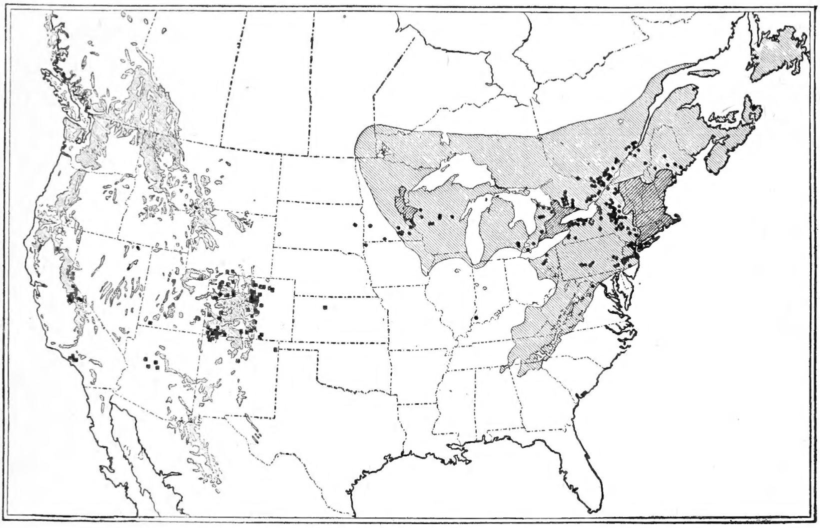

FIG. 2.—Outline map of the United States, showing the known distribution of *Cronartium ribicola* and *C. occidentale* in North America to January 1, 1920. Localities for *Cronartium occidentale* are shown by black squares in the Pacific coast and Rocky Mountian regions, the easternmost point being in western Kansas. This is where it was found in 1892, but it has not been seen there since. Localities for *C. ribicola* are indicated by double cross hatching and black dots, nearly all being north of the Potomac and Ohio Rivers and east of the Mississippi River. Four points in southwestern Minnesota, eastern South Dakota, and northern Iowa were found to be due to diseased nursery stock which was shipped in. It is believed that the disease now has been eradicated in these outer western localities. The natural distribution of the eastern white pine is shown in the large cross-hatched area mostly east of the Mississippi River. The cross-hatched areas shown on the western half of the map indicate the known distribution of the western white pines. The piñon pines range as far north as southern Idaho but at altitudes different from those of the white pines. *Cronartium ribicola* is limited to the eastern white-pine area and was not known in North America until 1906. In most places where now found it has been traced to diseased imported white-pine stock. *Cronartium occidentale* is limited to that part of the western white-pine area in which piñon pines are native, where it appears also to be native. The two fungi are separated by a strip of prairie country about 500 miles wide. Distribution of the pines furnished by the Forest Service, United States Department of Agriculture. Distribution of *Cronartium occidentale* furnished by Messrs. Bethel and Posey, of the Offices of Investigations in Forest Pathology and of Blister-Rust Control, respectively.

To sum up briefly: *Pinus cembra*, the probable original pine host, ranges across northern Asia; and the fungus is reported from western, eastern, and central Asia, in some places where it may easily be endemic.

In North America, *Cronartium ribicola* was first found in 1906 at Geneva, N. Y. (3, 150). Later findings have indicated that it was here in the Northeastern States as early as 1898 (108, 136, p. 6). It might have been in North America a few years, but not many, before that date. This is supported by Clinton (13), who unsuccessfully examined specimens of Ribes which are in some of the larger herbaria of the eastern part of this country. The writer has supplemented Clinton's work by examining the Ribes specimens in several additional herbaria. These include the Pringle herbarium at the University of Vermont and the local collections of the University of Vermont; of Dartmouth College; of President Ezra Brainerd, of Middlebury College; of Mr. C. A. Weatherby, of East Hartford, Conn.; and of Mr. C. H. Bissell, of Southington, Conn. The most notable herbarium examined was that of the Boston Society of Natural History, which contains many New England collections made in the early years of the nineteenth century. Moreover, such keen fungus collectors as Farlow, Seymour, G. P. Clinton, Peck, Ellis, George Clinton, Stewart, and many others, never collected *Cronartium ribicola* until 1906, showing that it is a recent immigrant. Since 1909, when it was first found in North America on white pines, *Cronartium ribicola* has spread until it is firmly estab-

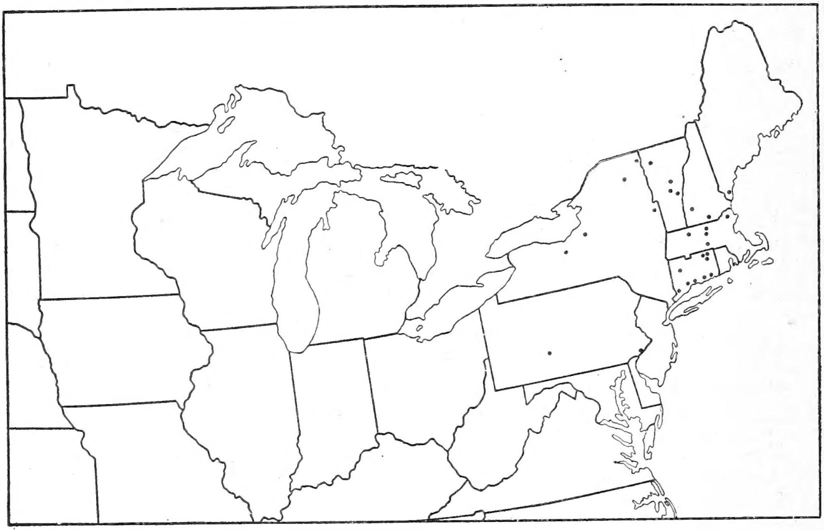

FIG. 3.—Outline map of the northeastern part of the United States, showing (by black dots) the known distribution of white-pine blister rust in North America to and including 1909.

lished in New England, New York, Wisconsin, Minnesota, and Canada.

It has been known since 1892 that there was a fungus on Ribes in the West much resembling *Cronartium ribicola*, but until 1917 its alternate stage on pines was unknown. In that year the Office of Investigations in Forest Pathology began work upon this western fungus, which was soon found to have an alternate stage on *Pinus edulis* and *P. monophylla* in Colorado and Arizona (50, 114) and was named *Cronartium occidentale*. Its distribution and that of *C. ribicola* as known to January 1, 1920, is shown on the map (fig. 2). See figures 3 to 12 for the progress of *C. ribicola* by years from 1909 to 1918, inclusive. *Cronartium occidentale* is found in localities where it could hardly be an introduction, as the Ute Indian Reservation in southwestern Colorado, where it was found by Bethel in 1897; also in the Mesa Verde region, where no cultivated Ribes or pines have ever been introduced. *Ribes aureum* is native in the Rocky Mountain region and is a favorite host for *Cronartium occidentale* as well as *C. ribicola*.

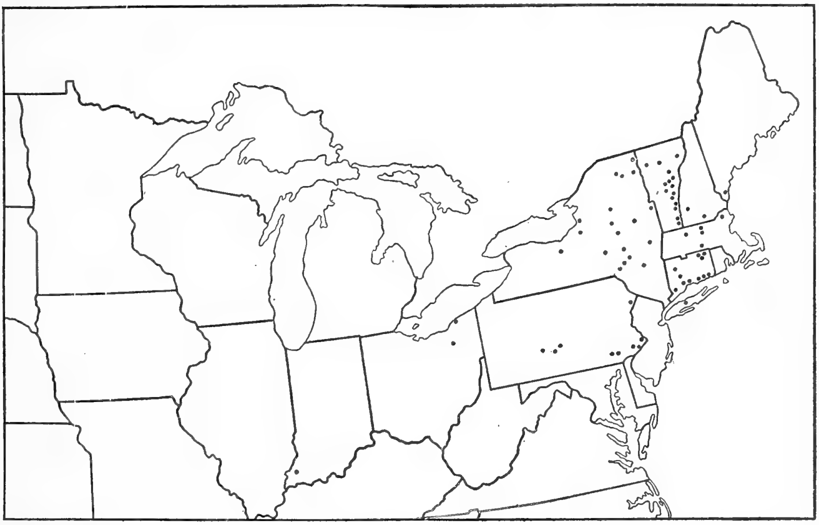

FIG. 4.—Outline map of the northeastern part of the United States, showing (by black dots) the known (cumulative) distribution of white-pine blister rust in North America to and including 1910.

Since *Ribes aureum* was intimately associated with *Cronartium ribicola* in its earlier known occurrences in Europe, an inquiry has been made into the possibility of the fungus being American in origin and its being introduced into Europe on *R. aureum* when that plant was first sent there. The facts thus far determined are[2] that *R. aureum*

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[2] Spaulding, Perley. Ribes aureum not an original host of Cronartium ribicola. In manuscript. To be published in Phytopathology.

is definitely stated to have been introduced into England (the probable first point of introduction in Europe) in 1812 by Thomas Nuttall. Evidently Nuttall collected the seeds of this plant while on a botanical trip in 1811 with John Bradbury up the Missouri River to a point in the eastern part of Mercer County, N. Dak. His material must have been shipped quite promptly to England, as Fraser's nursery at

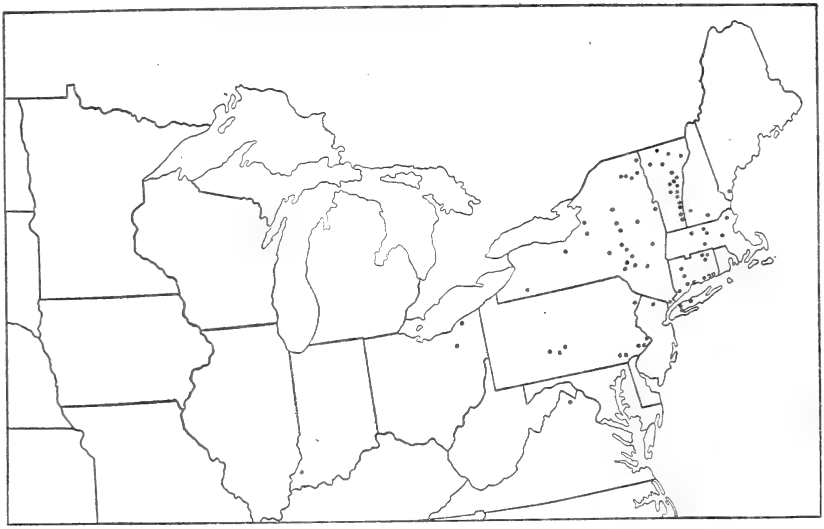

FIG. 5.—Outline map of the northeastern part of the United States, showing the known distribution of white-pine blister rust in North America to and including 1911.

FIG. 6.—Outline map of the northeastern part of the United States, showing (by black dots) the known distribution of white-pine blister rust in North America to and including 1912.

Chelsea, London, in 1813, offered for sale plants "collected in Upper Louisiana and principally on the River Missourie, North America." There is reason to believe that these were Nuttall's plants. The plant of interest to us is listed as *Ribes longiflorum,* a new species from the Missouri. This is now known as *R. odoratum* Wendland, which is the common form generally cultivated in the eastern United

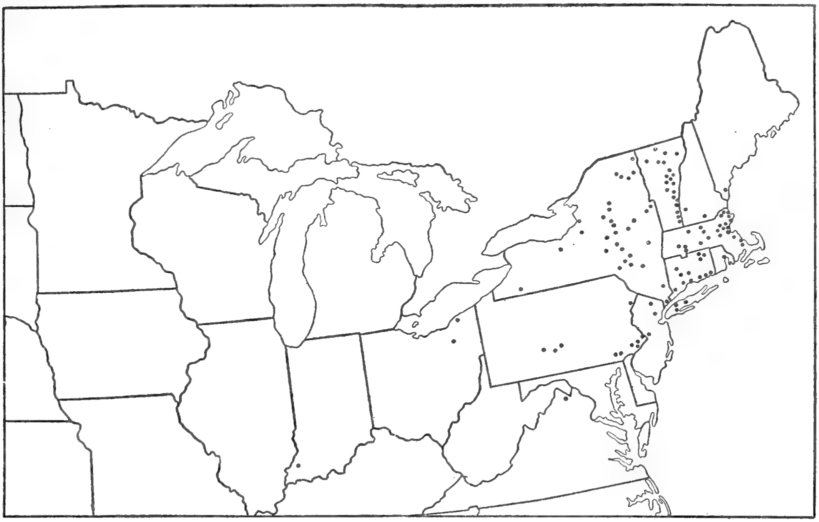

FIG. 7.—Outline map of the northeastern part of the United States, showing (by black dots) the known distribution of white-pine blister rust in North America to and including 1913.

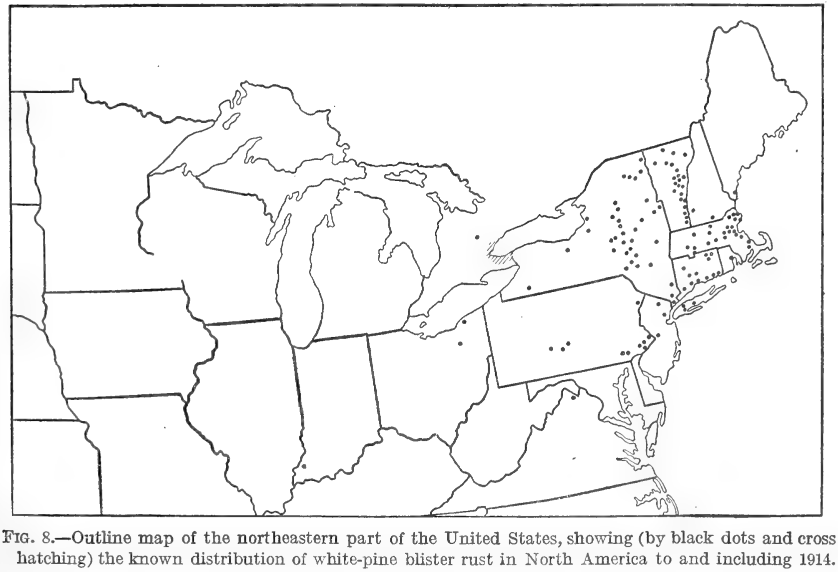

FIG. 8.—Outline map of the northeastern part of the United States, showing (by black dots and cross hatching) the known distribution of white-pine blister rust in North America to and including 1914. The cross hatching in this and the following maps indicates areas which are generally infected.

States under the name *R. aureum*. This appears to be the form most common in cultivation in Europe, but the true *R. aureum* of the Rocky Mountain region and the plains of the Columbia was evidently introduced there soon after *R. odoratum*, if not at about the same time. Pursh may have referred to living plants of true *R. aureum* but we have no means of determining this. Lindley in 1828 made the new species *R. tenuiflorum* (now *R. aureum*) and says "Clt. 1812," evidently meaning "cultivated in 1812." He had this so definitely distinguished from our *R. odoratum* that his statement is fairly conclusive that *R. aureum* actually was introduced into England the same year as was *R. odoratum*. The agent introducing *R. aureum* can not be determined beyond question. There appears to be little doubt, because of the difficulty of communication at that time, that both plants were carried from their native regions to the eastern part of this country in the form of seeds. Cuttings may have been sent to Europe but it is more likely that seeds were sent. Seeds would not be likely to transmit a rust which does not attack the fruit. It does not seem possible that a fungus like *Cronartium ribicola* could be carried to Europe on these plants without becoming established in the Eastern States. Moreover, these species of Ribes apparently were introduced into Great Britain first. The fungus was not known in Great Britain until 1892, long after it was prevalent in other northern European countries. It appears that *Cronartium ribicola* was carried to Great Britain on infected white pines from northwestern Germany. The evidence appears to show that *Cro-*

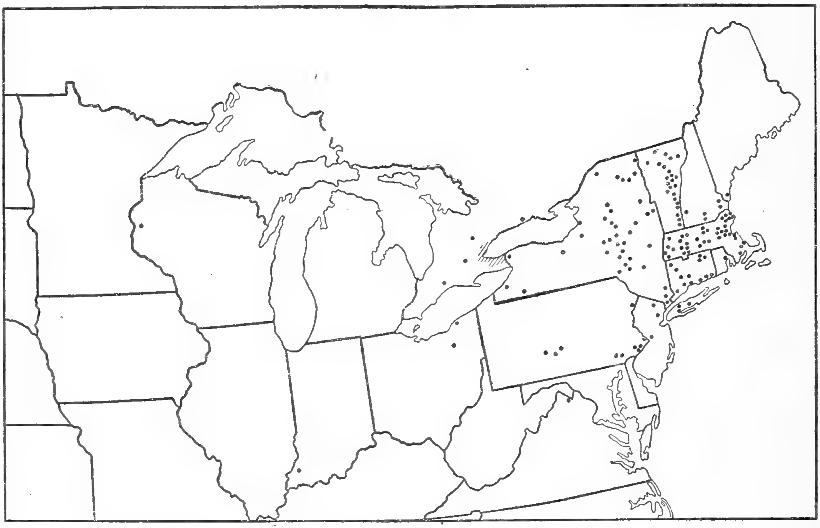

FIG. 9.—Outline map of the northeastern part of the United States, showing (by black dots and cross hatching) the known distribution of white-pine blister rust in North America to and including 1915.

nartium ribicola attacked *Ribes aureum* and *R. odoratum* after they reached Europe. Their susceptibility also indicates that they are not original hosts of the fungus.

Summing up the evidence available, it appears (1) that *Cronartium ribicola* is Asiatic in origin; (2) that it spread in the early 1800's into western Russia, whence it eventually spread well over Europe (41); (3) that it was brought to North America in young trees of *Pinus strobus;* and (4) that comparative studies (50) show that *Cronartium occidentale* is distinct.

HOSTS OF CRONARTIUM RIBICOLA.

Pines Infected and Likely to Become Infected.

Cronartium ribicola has attacked 11 of the white pines in the countries, Provinces, and States indicated in the following list:

Pinus aristata Engelmann in England (20a).
  ayacahuite Ehrenb. in Scotland and England.[3]
  cembra L. in Russia (58, 93), Switzerland (39, 40, 123, Germany (72, 77, 174, 177), U. S. A. (Mass., Minn.).[4]
  excelsa Wall. in Denmark (120), Germany (99), U. S. A. (Mass.).
  flexilis James in Germany (173), Sweden,[5] U. S. A. (Mass., Minn., Iowa).
  koraiensis Sieb. and Zucc. in Sweden.[5]
  lambertiana Douglas in Belgium (101), Germany (62, 173).
  monticola Douglas in Belgium (101), England (79), Germany (70).
  parviflora Sieb. and Zucc. in U. S. A. (Mass.).
  peuce Gris. in Germany (173).
  strobus L. in Austria-Hungary (178), Belgium (70), Denmark (81, 115, 117, 119, 120), Finland (54, 83), Switzerland (40), France (70), Germany (70), Great Britain (111), Holland (70), Ireland (42), Norway (70), Russia (27, 58, 120), Siberia (161), Sweden (131[5]), Canada—Ontario (23, 56) and Quebec (107, 121), U. S. A. (Conn., Ind., Iowa, Maine, Mass., Mich., Minn., N. H., N. J., N. Y., Ohio, Penn., R. I., S. Dak., Vt., Va., Wis.). The fungus has occurred in a number of these States only on diseased pines shipped from outside points.

In every case the disease attacked these pines naturally in outbreak areas of Europe and North America and is not known to attack any of the pitch pines, although some of them have been present in infected areas. Whenever the other white pines are continuously exposed to the fungus they will be likely to develop the disease. The blister rust was first found on the different species of pines as follows:

Pinus strobus. Russia in 1854.
  lambertiana. Germany in 1887.
  cembra. Russia in 1890.
  monticola. England in 1898.
  excelsa. Denmark in 1902.
  aristata. England in 1907.

Pinus ayacahuite. Great Britain in 1908.
  flexilis. Germany in 1914.
  peuce. Germany in 1914.
  parviflora. United States in 1916.
  koraiensis. Sweden in 1920.

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[3] Communicated in a private letter from Dr. A. B. Borthwick, of Scotland.

[4] The statements concerning occurrences in North America are based on records and specimens in the Office of Investigations in Forest Pathology.

[5] Private letter from W. Stuart Moir, Office of Blister-Rust Control.

Sudworth (154) recognizes eight species of the white pines (exclusive of the piñon pines) for North America (fig. 2) but does not treat those of the Old World. Shaw (126), who treats the pines of the world, also recognizes eight North American species of white pines. He is, therefore, taken as the authority for the pines in this bulletin. The white pines of the world are grouped by Shaw as follows:

- Genus Pinus.
    - Section Haploxylon.
        - Subsection Cembra.
            - Group I. Cembræ.
                - *koraiensis* +.
                - *cembra* +.
                - *albicaulis*.
            - Group II. Flexiles.
                - *flexilis* +.
                - *armandi*.
            - Group III. Strobi.
                - *ayacahuite* (or *strobiformis*) +.
                - *lambertiana* +.
                - *parviflora* +.
                - *peuce* +.
                - *excelsa* +.
                - *monticola* +.
                - *strobus* +.
        - Subsection Paracembra.
            - Group IV. Cembroides—piñon pines.
            - Group V. Gerardianæ—piñon pines.
            - Group VI. Balfourianæ.
                - *balfouriana*.
                - *aristata*+.

In examining the above synopsis, note the grouping of the known susceptible species (which are indicated by +) especially in the first three groups which make up the subsection Cembra. Investigations of outbreak areas in Europe where the various species of pine have been present might yield on this point most interesting and valuable information which can be obtained in no other way.

Inoculations of Cronartium Ribicola on Pines.

Klebahn (68, 71) appears to be the first European investigator who has inoculated pines with *Cronartium ribicola* and who has published his results. He inoculated young *Pinus strobus* trees with pycnospores, but with no success (70, p. 387). Inoculations made by him with sporidia in 1888 were rendered worthless because the pines were probably infected naturally before the test was made (71). On August 27, 1903, Klebahn (71) made inoculations on two young *Pinus strobus* trees by suspending telia-bearing leaves of *Ribes nigrum* above the trees and covering them with a large bell jar. On June 19, 1904, the pines were examined. At that time some of the new shoots bore abnormal leaves of a juvenile type singly, instead of in fives. The new twigs were abnormally pale in color. Many of the leaves of the growth of the previous year were spotted with yellow through their entire thickness. These yellow spots were especially plentiful near the base of the leaves. Microscopic examination showed abundant mycelium to be present in the yellow areas. Later pycnia developed on the twigs near the bases of the spotted leaves.

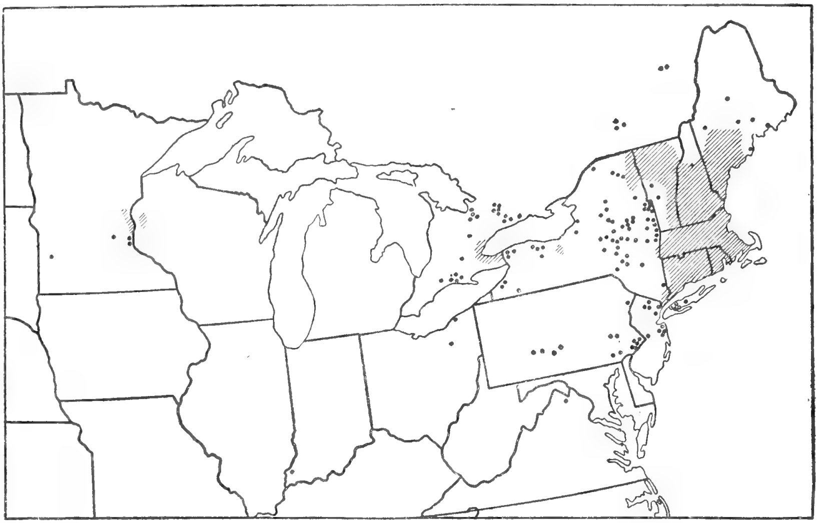


FIG. 10.—Outline map of the northeastern part of the United States, showing (by black dots and cross hatching) the known distribution of white-pine blister rust in North America to and including 1916.

In 1914, Tubeuf (174) inoculated trees of *Pinus strobus*, *P. lambertiana*, *P. cembra*, *P. cembroides*, *P. excelsa*, *P. peuce*, *P. parviflora*, *P. flexilis*, and *P. montezumae* with sporidia of *Cronartium ribicola* under controlled conditions. In 1917, æcia were produced on some of the *P. strobus*. Yellow spots were produced on the leaves of *P. lambertiana*, but no further development of the fungus occurred. Spots which were doubtfully caused by the fungus were noted on *P. cembroides*. No other species became infected. Infections were produced directly on the juvenile leaves, on mature leaves, and through the epidermis of the lengthening buds of the young shoots.

In North America, the writer seems to have been the first to inoculate successfully young *Pinus strobus* trees with sporidia (133, 134). The inoculations were made both with and without wounds in the young bark, telial columns being used for inoculum. Pycnial drops were produced by one tree unwounded and by one which was wounded. At this stage slugs ate the infected bark and prevented further development of the fungus. In 1916 and in 1917, 150 æciospore inoculations were made on leaves, on twigs of various ages, and on branches of *P. strobus* trees up to six years. No infections have resulted.

Clinton and Miss McCormick (14, 15), have published details of successful inoculations, through the leaves, with sporidia on *P. strobus.* Inoculations were unsuccessful upon leaves of *P. excelsa, P. flexilis, P. koraiensis,* and *P. cembra;* also on the pitch pines *P. resinosa, P. sylvestris, P. densiflora,* and *P. austriaca.* Yellow spots have been secured on leaves of *P. lambertiana, P. pinea,* and *P. sabiniana.*

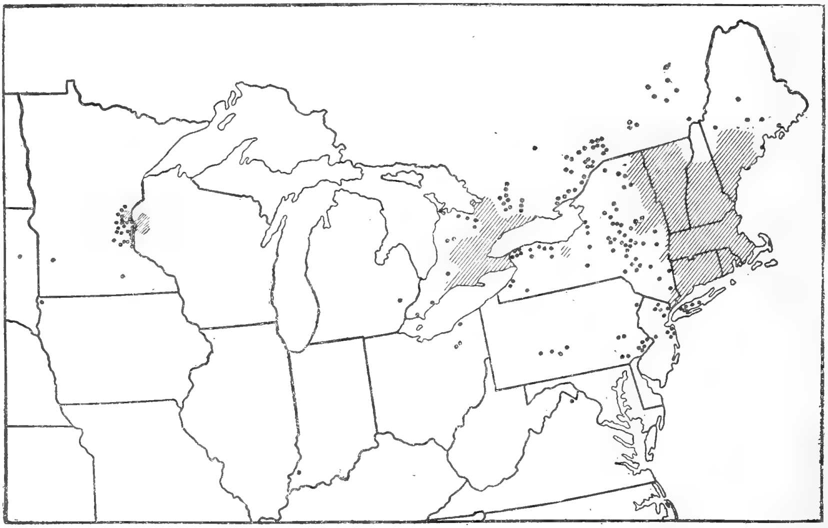


FIG. 11.—Outline map of the northeastern part of the United States, showing (by black dots and cross hatching) the known distribution of white-pine blister rust in North America to and including 1917.

Cross-inoculations that are known to have been successful up to July 1, 1920, are shown in Plate I.

Species of Ribes That Have Been Infected Naturally.

In Europe and North America, where extensive outbreaks of *Cronartium ribicola* have occurred, a considerable number of species of Ribes have been found naturally infected by the fungus. Practically all of the cultivated species and most of the wild ones take the disease in every extensive outbreak area. More species have been found infected in Europe than in North America, because outbreaks have been discovered there in botanical gardens, parks, and nurseries where extensive collections of the different species of Ribes were located, and hence more species have been subjected to attack.

In Europe the following species have become infected naturally: *Ribes aciculare* Smith, *R. affine* H. B. K., *R. alpinum* L., *R. americanum* Mill., *R. aureum* Pursh, *R. biebersteinii* hybrid, *R. bracteosum* Douglas, *R. cynosbati* L., *R. divaricatum* Douglas, *R. glandulosum* Grauer, *R. gordonianum* hybrid, *R. hirtellum* Michx., *R. irriguum* Douglas, *R. menziesii* Pursh, *R. missouriense* Nuttall, *R. multiflorum* Kit., *R. nigrum* L., *R. niveum* Lindl., *R. odoratum* Wendl., *R. oxyacanthoides* L., *R. petraeum* Wulf., *R. reclinatum* L., *R. rotundifolium* Michx., *R. rubrum* L., *R. sanguineum* Pursh, *R. setosum* Lindl., *R. triste* Pallas, *R. vulgare* Lam.

The names of species of Ribes of North America are based on the treatment of the North American species by Coville and Britton in "North American Flora" (22) and of species of the other continents on that of Janczewski in "Monographie des Groseilliers, Ribes L." (60). For the sake of convenience the currants and gooseberries are kept in the single genus Ribes.

As recently as 1914 (136) the fungus had not been found in North America attacking any wild species of Ribes. Since then it has been found attacking an increasing number of wild Ribes, as additional species are subjected to infection by the spreading and multiplication of the known outbreak areas and as new ones are discovered. To date it is known to have been found attacking naturally the following species of Ribes in the States and Provinces named:

Ribes americanum (*floridum*).—Maine, New Hampshire, Vermont, Massachusetts, Rhode Island, New York, Wisconsin, Minnesota, and Ontario.

cynosbati.—Maine, New Hampshire, Vermont, Massachusetts, Rhode Island, Connecticut, New York, New Jersey, Wisconsin, Minnesota, and Ontario.

glandulosum (*prostratum*).—Maine, New Hampshire, Vermont, Massachusetts, Connecticut, New York, Wisconsin, Minnesota, and Ontario.

hirtellum.—Maine, New Hampshire, Massachusetts, New York, Wisconsin, and Minnesota.

irriguum.—New York.

lacustre.—Maine, New Hampshire, New York, and Wisconsin.

missouriense.—New York, Minnesota, and Wisconsin.

nigrum.—Maine, New Hampshire, Vermont, Massachusetts, Rhode Island, Connecticut, New York, New Jersey, Wisconsin, Minnesota, Ontario, and Quebec.

odoratum.—Maine, New Hampshire, Vermont, Massachusetts, Rhode Island, Connecticut, New York, Minnesota, and Ontario.

reclinatum (*grossularia*).—Maine, Vermont, Massachusetts, New York, Wisconsin, Minnesota, and Ontario.

rotundifolium.—New York.

triste.—Maine, New Hampshire, Massachusetts, Wisconsin, Minnesota, and Ontario.

vulgare (*rubrum*).—Maine, New Hampshire, Vermont, Massachusetts, Rhode Island, Connecticut, New York, Wisconsin, Minnesota, and Ontario.

Inoculations of Cronartium ribicola on Ribes.

In 1888, Klebahn (63, 64) made the first known successful inoculations of this fungus on Ribes. Since that time a number of inoculations have been made in Europe by Klebahn (65, 66, 67, 68, 69, 70), Wettstein (70), Rostrup (118, 119, 120), Schøyen (124), Eriksson (31, 33), Tubeuf (167), Hennings (53), Sorauer (129), Tranzschel (92), Neger (100), Ewert (36, 37), Naumann (36), and Jaczewski (58, 59). The published accounts of most of these experiments are very fragmentary and lack many essential details. In fact the attitude of the European investigators seems to have been that of mild interest in a new fungus rather than that of intensive study of a new parasite and of the destructive disease caused by it.

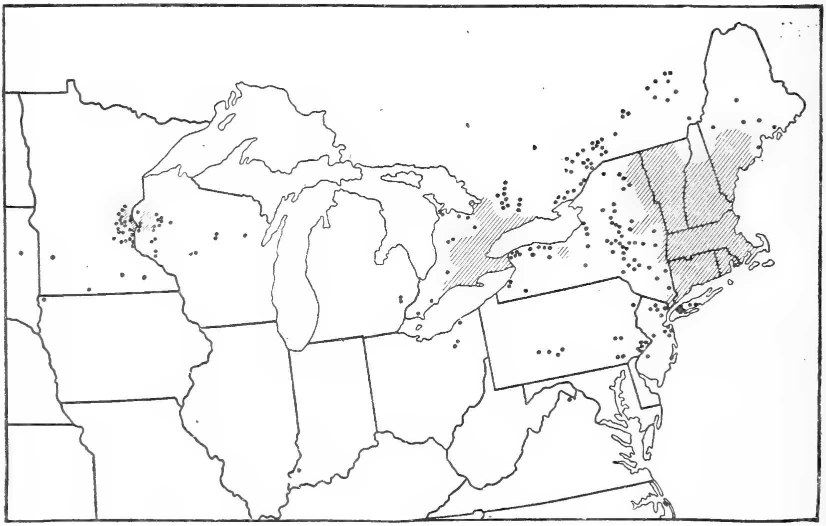
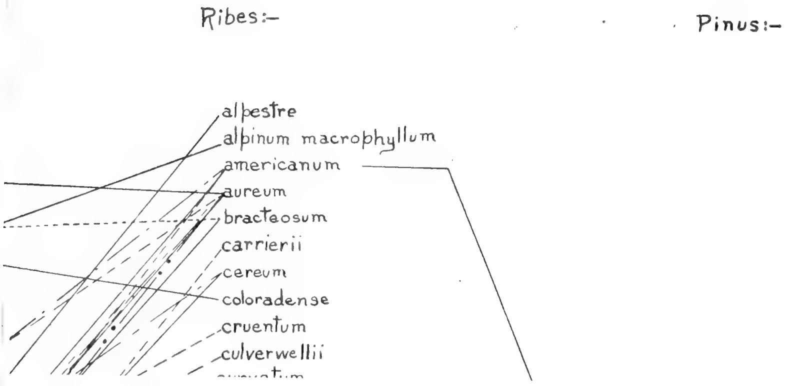


FIG. 12.—Outline map of the northeastern part of the United States, showing (by black dots and cross hatching) the known distribution of white-pine blister rust in North America to and including 1918. For distribution to the end of 1919, see figure 2.

Since the summer of 1909 the writer and his collaborators have made repeated tests under controlled and natural conditions of all species and of all varieties of the cultivated species of Ribes that could be obtained. In the earlier work complete records were not kept, but in the last few years the records were made to cover all points likely to be of value. Hundreds of inoculations have been made on the more susceptible species to keep the fungus growing in vigorous condition, without records being made. It was felt that greenhouse tests alone were not dependable for susceptibility data. Therefore, in 1916, a test plat was located upon Block Island, R. I. This island lies 12 miles from the nearest projecting point of the mainland and 15 miles or more from the main shore line. No white pines are on the island and but few cultivated Ribes. It was chosen

PLATE I.


Ribes:-
Pinus:-
alpestre
alpinum macrophyllum
americanum
aureum
bracteosum
carrierii
cereum
coloradense
cruentum
culverwellii

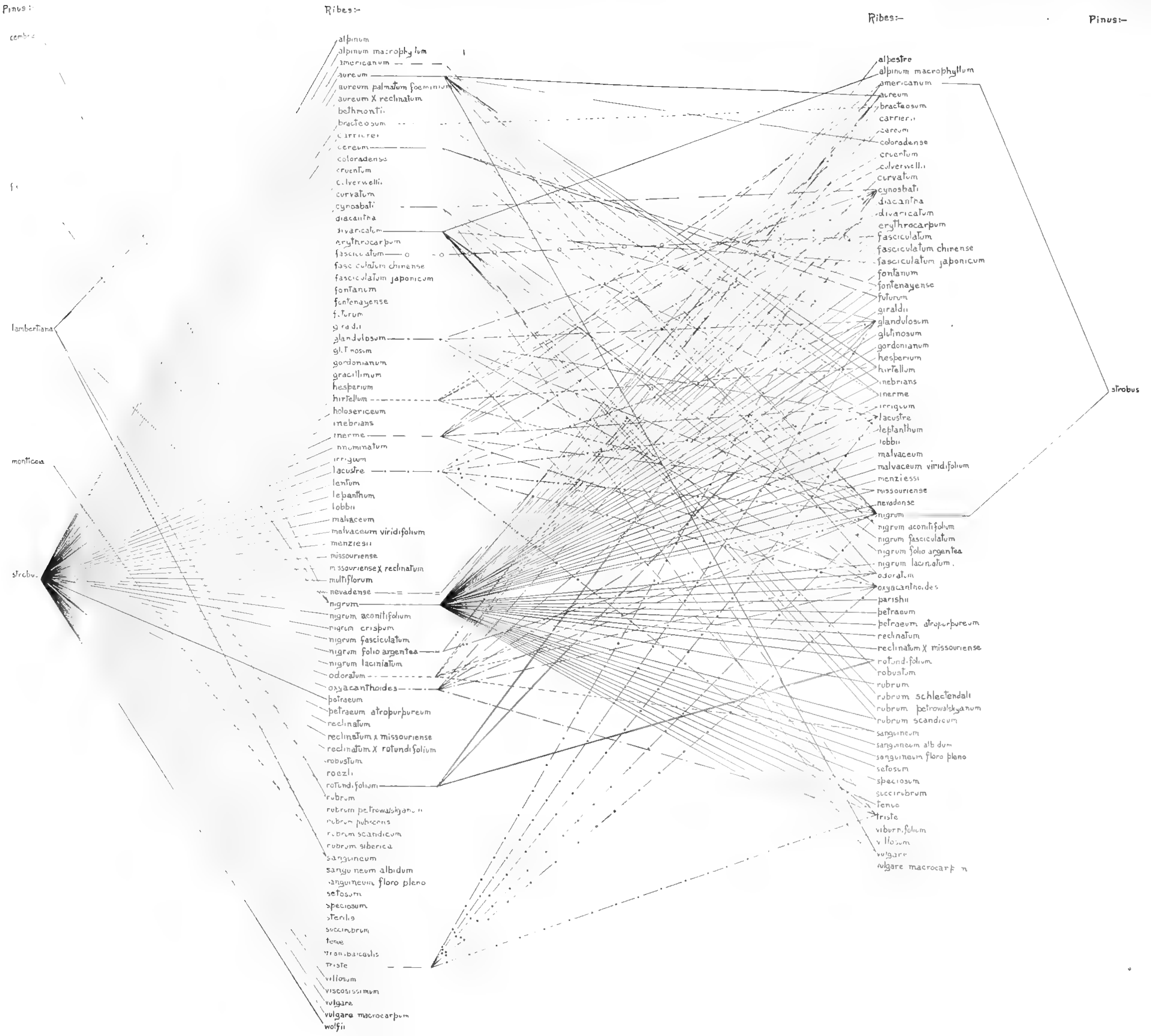


DIAGRAM SHOWING CROSS-INOCULATIONS MADE WITH CRONARTIUM RIBICOLA TO JANUARY, 1921, INCLUDING THOSE MADE BY EUROPEAN INVESTIGATORS.

Drawn by Rush P. Marshall.

46103°—21. (To face page 16.)

as the safest place for such work at that time. In midsummer, 1916, before the disease was fairly started on the bushes on the island, it was found to be pretty generally distributed over New England on Ribes, having plainly been widely disseminated there before the Block Island experiment was started. Conditions on the island are not very favorable for Ribes and are decidedly unfavorable for white pines. *Pinus nigra* var. *austriaca* is the only pine seen on the island, and it occurs only in protected hollows.

Table I presents the general results of tests made in the greenhouse where inoculations were made with both æciospores and urediniospores. A preliminary statement has been published, giving the earlier results of this work (147). This table is to be interpreted as follows:

In the columns headed "Susceptibility," a single cross (×) means slight infection, two crosses (××) mean a medium degree of infection, and three crosses (×××) mean heavy infection.

There are no means of knowing what degree of susceptibility was indicated by the experiments of European and Canadian investigators, whose results are included in section 1 of Table I. The foreign experimenters are first listed alphabetically under each species of Ribes, then the work done in this country is given in a similar manner. The varietal tests (sections 2 to 4 of Table I) are wholly the work of the Office of Investigations in Forest Pathology, there being practically no data in foreign literature on inoculations of horticultural varieties.

In numerous cases but a single test has been made as yet; but the general behavior of the tested plants in the spread of the fungus, the type of its fruiting, etc., during the rest of the season are considered in the final estimate of susceptibility. When a single test has been made under favorable conditions, it is believed that the results are fairly indicative of the susceptibility of the species or variety tested. Many tests were made under conditions known to be adverse, and the negative results are largely due to this cause alone. But these tests are given with the others to give some idea of what has been done. Scanty numbers of tests are often due to the Ribes stock dying before a second test could be made. This is true of many cuttings which made a weak start and did not survive potting.

In sections 2 to 4 of Table I, relating to the varieties of Ribes, an attempt has been made to use varietal names that are intelligible to horticulturists as accepted by the American Pomological Society. Acknowledgment is made to the Office of Horticultural and Pomological Investigations of the United States Department of Agriculture for help in this matter. In some cases varietal names are given which are considered to be synonyms of others in the list; but in such cases the stocks used under the two names were evidently different. Varieties and even species of Ribes supplied by nurserymen are often other than what they purport to be, and in some cases they are mixtures of two or more distinct things; hence, the varietal names can not be taken as being absolutely reliable.

TABLE I.—*Results of inoculations made on various species and horticultural varieties of Ribes, showing data on susceptibility in the greenhouse and out of doors on Block Island, R. I.*

Species or variety and investigators.	Inoculations.		Susceptibility.	
	Infection.	Number.	In the greenhouse.	Out of doors.
SEC. 1.—*Species of Ribes*.[a]				
R. alpestre:				
Gravatt	2	2	××	××
R. alpinum:				
Klebahn	1	1	....	....
Neger	0	1	....	....
Sorauer	1	1	....	....
Gravatt	0	1	0	0
Marshall	0	2		
Taylor	0	2		
R. alpinum macrophyllum:				
Rhoads	0	1	0	....
Spaulding	0	1		
R. amarum:				
Taylor	1	1	×××	....
R. americanum:				
Sorauer	1	1	....	....
Gravatt	4	4	××	××
Spaulding	2	2		
Taylor	6	6		
York	1	1		
R. aureum:				
Klebahn	4	4	....	....
Sorauer	1	1	....	....
Tubeuf	1	1	....	....
Gravatt	13	13	××	××
Hedgcock	1	1		
Marshall	5	6		
Spaulding	6	6		
Taylor	27	28		
R. aureum "palmatum foeminum":				
Spaulding	1	2	××	....
R. aurem × reclinatum:				
Gravatt	1	1	×	....
R. bethmontii:				
Spaulding	1	2	××	....
R. bracteosum:				
Gravatt	3	4	××	×
R. carrierei:				
Gravatt	10	11	××	××
R. cereum:				
Gravatt	2	2	××	×
Marshall	2	2		
Spaulding	6	7		
Taylor	2	3		
R. coloradense:				
Spaulding	1	1	××	....
Taylor	2	2		
R. cruentum:				
Gravatt	5	7	××	....
R. culverwellii:				
Gravatt	3	4	××	×
Marshall	3	3		
R. curvatum:				
Gravatt	1	4	××	××
Marshall	1	3		
Spaulding	1	1		
Taylor	1	1		
R. cynosbati:				
Tubeuf	1	1	....	....
Gravatt	3	4	××	....
Hedgcock	1	1		
Lyman	2	3		
Spaulding	2	2		
SEC. 1—*Species of Ribes*—Contd.				
R. diacantha:				
Gravatt	1	2	×	....
Taylor	0	2		
R. divaricatum:				
Rostrup	1	1	....	....
Tubeuf	1	1	....	....
Gravatt	11	18	××	××
Spaulding	3	3		
Taylor	2	2		
R. erythrocarpum:				
Gravatt	2	2	××	....
R. fasciculatum:				
Gravatt	4	4	××	×
Merrill	1	2		
Spaulding	1	3		
Taylor	20	20		
R. fasciculatum chinense:				
Gravatt	1	1	×	....
Merrill	1	3		
Spaulding	6	6		
R. fasciculatum japonicum:				
Spaulding	2	2	××	....
R. fontanum:				
Colley and Taylor	1	1	××	....
Gravatt	1	1		
R. fontenayense:				
Gravatt	3	3	×	×
R. futurum:				
Gravatt	1	1	××	....
Merrill	1	1		
Spaulding	1	1		
Taylor	1	1		
R. giraldii:				
Gravatt	1	1	××	....
R. glandulosum:				
Lyman	1	1	××	....
Snell	6	6		
Spaulding	1	1		
Taylor	2	2		
R. glutinosum:				
Gravatt	1	3	×	....
Spaulding	2	2		
R. gordonianum:				
Gravatt	3	4	××	××
Spaulding	1	1		
R. hesperium:				
Gravatt	1	2	××	....
Merrill	1	1		
Taylor	1	1		
R. hirtellum:				
Gravatt	7	11	××	×
Lyman	2	2		
Spaulding	2	4		
Taylor	2	3		
R. hirtellum × reclinatum:				
Hedgcock	2	2	×	....
R. holosericeum:				
Gravatt	1	1	××	....
R. inebrians:				
Hedgcock	4	4	×	....
R. inerme:				
Gravatt	15	17	××	....
Hedgcock	2	2		
Spaulding	2	3		
Taylor	4	4		

[a] Summary of tests made in foreign countries and in America.

TABLE I.—*Results of inoculations made on various species and horticultural varieties of Ribes, etc.*—Continued.

Species or variety and investigators.	Inoculations.		Susceptibility.	
	Infection.	Number.	In the greenhouse.	Out of doors.
SEC. 1.—*Species of Ribes*—Contd.				
R. innominatum:				
Spaulding	1	4	××	....
Taylor	2	2		
R. irriguum:				
Gravatt	2	2	×	×
R. lacustre:				
Gravatt	8	11	××	×
Spaulding	2	2		
Taylor	3	3		
R. leptanthum:				
Gravatt	4	5	[b] ×	....
Spaulding	1	1		
Taylor	4	7		
R. lobbii:				
Gravatt	2	4	×	×
R. malvaceum:				
Gravatt	1	4	×	....
Spaulding	0	3		
R. malvaceum viridifolium:				
Gravatt	1	4	×	....
Merrill	1	2		
Spaulding	0	3		
R. menziesii:				
Gravatt	1	1	××	×
Taylor	4	4		
R. missouriense:				
Rostrup	1	1	....	....
Gravatt	1	1	××	×
Lyman	1	1		
Spaulding	1	1		
Taylor	3	3		
R. missouriense × reclinatum:				
Gravatt	2	3	×	....
R. montigenum:				
Spaulding	1	1	×	....
R. multiflorum:				
Rostrup	1	1	....	....
Rhoads	0	1	×	....
Spaulding	1	1		
R. nevadense:				
Gravatt	0	1	××	....
Spaulding	2	2		
R. nigrum:				
Eriksson	18	18	....	....
Ewert	6	6	....	....
Hennings	1	1	....	....
Klebahn	11	12	....	....
Jaczewski	1	1	....	....
McCubbin	3	4	....	....
Naumann	1	1	....	....
Rostrup	1	1	....	....
Sorauer	1	1	....	....
Tranzschel	1	1	....	....
Tubeuf	2	2	....	....
Gravatt	29	36	×××	×××
Hedgcock	3	3		
Marshall	3	3		
Merrill	5	5		
Spaulding	8	8		
Taylor	11	21		
York	1	1		
R. nigrum "aconitifolium":				
Spaulding	1	1	××	....
R. nigrum "crispum":				
Sorauer	1	1	....	....
R. nigrum "fasciculatum":				
Rhoads	1	1	×××	....
R. nigrum "folio argentea":				
Spaulding	1	1	×××	....
Taylor	2	2		
R. nigrum "laciniatum":				
Sorauer	1	1	....	....
R. odoratum:				
Gravatt	25	29	××	××
Hedgcock	6	6		
Marshall	1	2		
Spaulding	3	3		
Taylor	15	15		
R. oxyacanthoides:				
Tubeuf	0	1	....	....
Gravatt	2	2	××	....
Lyman	0	1		
Merrill	1	1		
Spaulding	1	1		
Taylor	2	2		
R. parishii:				
Taylor	7	7	××	....
R. petraeum:				
Gravatt	2	3	××	....
Spaulding	1	1		
R. petraeum atropurpureum:				
Gravatt	1	1	××	....
R. reclinatum:				
Jaczewski	0	1	....	....
Klebahn	1	1	....	....
Schøyen	1	1	....	....
Sorauer	0	1	....	....
Tubeuf[c]	1	1	....	....
Gravatt	4	4	×	×
Hedgcock	1	1		
Spaulding	1	1		
R. reclinatum grafted on R. aureum:				
Klebahn	6	7	×	....
R. reclinatum × missouriense:				
Gravatt	2	2	××	××
R. reclinatum × rotundifolium:				
Gravatt	1	1	×	....
R. robustum:				
Spaulding	1	2	××	....
Taylor	2	2		
R. roezli:				
Gravatt	0	1	×	....
Taylor	1	1		
R. rotundifolium:				
Sorauer	1	1	....	....
Gravatt	1	1	××	×
Spaulding	[c] 0	8		
Taylor	[c] 6	6		
R. rubrum:				
Jaczewski	0	1	....	....
Klebahn	1	1	....	....
Neger	0	1	....	....
Rostrup	1	1	....	....
Sorauer	1	1	....	....

[b] Slight.

[c] Part seedling plants.

TABLE I.—*Results of inoculations made on various species and horticultural varieties of Ribes, etc.*—Continued.

Species or variety and investigators.	Inoculations.		Susceptibility.	
	Infection.	Number.	In the greenhouse.	Out of doors.
SEC. 1.—*Species of Ribes*—Contd.				
R. rubrum "petrowalskyanum":				
Spaulding	0	1	×	....
Spaulding and Merrill	1	1		
R. rubrum pubescens:				
Spaulding	1	2	×	....
R. rubrum scandicum:				
Merrill	2	2	××	....
Rhoads	1	1		
Spaulding	1	1		
Taylor	1	1		
R. rubrum "sibiricum":				
Spaulding and Merrill	2	3	×	....
R. sanguineum:				
Neger	1	1	....	....
Sorauer	1	1	....	....
Tubeuf	1	1	....	....
Gravatt	4	6	×	....
Spaulding	4	4		
Taylor	1	1		
R. sanguineum "albidum":				
Gravatt	6	6	××	××
R. sanguineum "floro pleno":				
Gravatt	1	1	×	×
Marshall	2	4		
R. setosum:				
Sorauer	1	1	....	....
Gravatt	3	4	×	....
Spaulding	1	1		
R. speciosum:				
Gravatt	3	7	××	×
Spaulding	1	1		
R. sterilis:				
Spaulding	0	2	0	....
R. succirubrum:				
Gravatt	1	2	××	××
Spaulding	0	1		
Taylor	1	1		
R. tenue:				
Gravatt	1	1	×××	....
Spaulding	0	1		
R. transbaicaulis:				
Spaulding and Merrill	1	1	×	....
R. triste:				
Spaulding	7	7	××	×
Taylor	0	1		
R. viburnifolium:				
Taylor	5	5	[b] ×	....
R. villosum:				
Gravatt	0	4	0	....
R. viscosissimum:				
Gravatt	3	3	××	....
R. vulgare:				
Schφyen	1	1	....	....
Hedgcock	3	3	×	....
Spaulding	1	1		
R. vulgare macrocarpum:				
Spaulding	1	1	×	....
R. wolfii:				
Spaulding	2	2	××	....

Species or variety and investigators.	Inoculations.		Susceptibility.	
	Infection.	Number.	In the greenhouse.	Out of doors.
SEC. 2.—*Varieties of Ribes nigrum.*				
Bang up:				
Gravatt	1	1	×	....
Beauty:				
Spaulding	1	1	×××	....
Black Dutch:				
Gravatt and Taylor	5	5	×××	....
"Black English":				
Colley, Gravatt, Spaulding, and Taylor	14	14	××	....
Black Grape:				
Spaulding	1	1	×	....
Blacksmith:				
Gravatt	3	3	××	....
Black Victoria:				
Gravatt, Marshall, and Spaulding	24	27	××	×××
Boskoop:				
Colley, Spaulding, and Taylor	5	8	××	××
Carter:				
Gravatt	4	4	××	××
"Cassis à fruit noir":				
Gravatt	2	2	××	××
Champion:				
Hedgcock, Marshall and Spaulding	5	5	×××	××
Climax:				
Gravatt, Marshall, Merrill, and Spaulding	14	14	×××	×××
Clipper:				
Gravatt	2	2	××	××
Collins:				
Spaulding	1	1	×	....
Coronation:				
Gravatt and Taylor	3	3	××	....
Eagle:				
Gravatt and Spaulding	13	13	××	××
Eclipse:				
Spaulding	2	2	×	....
Edina:				
Gravatt	4	4	×××	....
Ethel:				
Spaulding and Taylor	2	2	×	....
"French Black":				
Gravatt and Spaulding	4	4	××	××
Kerry:				
Gravatt	4	5	××	××
Lee:				
Gravatt, Marshall, and Spaulding	14	16	××	×××
Magnus:				
Gravatt	4	5	×××	×××
Mammoth:				
Gravatt	2	2	××	×××
Marvel:				
Gravatt, Spaulding, and Taylor	6	6	×	....
Naples:				
Marshall and Taylor	4	5	×××	×××
Norton:				
Gravatt	1	1	×	....

[b] Slight.

TABLE I.—*Results of inoculations made on various species and horticultural varieties of Ribes, etc.*—Continued.

Species or variety and investigators.	Inoculations.		Susceptibility.	
	Infection.	Number.	In the greenhouse.	Out of doors.
SEC. 2.—*Varieties of Ribes nigrum*—Con.				
Ontario: Gravatt	2	2	××	....
Saunders: Gravatt and Spaulding	6	9	××	×××
Seabrook: Spaulding	3	3	×××	....
Standard: Spaulding	1	1	×	....
Success: Spaulding	1	1	×	....
Topsy: Gravatt	2	2	××	....
Wales: Spaulding	1	1	××	....
Winona: Spaulding	1	2	×	....
Woods: Gravatt	4	4	×××	....
SEC. 3.—*Varieties of Ribes vulgare.*				
Admirable: Spaulding and Taylor	3	3	××	....
Albert: Gravatt and Marshall	4	18	×	×
Angers: Merrill and Spaulding	3	3	×	....
Bertin: Gravatt	2	2	×	....
"Blanc de Werden": Gravatt	4	4	×	....
Bonum: Gravatt	6	6	×	....
Brandenburg: Spaulding	2	2	××	....
Buddins: Gravatt	2	2	×	....
"Champagne White": Spaulding	1	1	×	....
Chautauqua: Gravatt and Marshall	7	7	×	××
Chenonceaux: Gravatt and Merrill	5	5	×	....
Cherry: Marshall	1	1	....	×
Comet: Marshall	2	2	....	×
"Commun Blanc": Gravatt	4	4	×	....
Conde: Spaulding	1	1	×	....
Constant: Gravatt	3	5	×	....
Crawford: Gravatt	2	2	×	....
Cumberland: Gravatt and Spaulding	5	5	×	0
Dilnot: Gravatt and Taylor	3	3	×	....
Diploma: Gravatt	6	7	×	×
Early Scarlet: Merrill and Spaulding	2	2	×××	....
SEC. 3.—*Varieties of Ribes vulgare*—Con.				
Everybodys: Gravatt	6	6	×	×
"Eyath Nova": Merrill and Spaulding	0	3	0	....
Fay: Gravatt	1	1	×	××
Filler: Gravatt	5	5	×	×
Fox Red: Gravatt	4	4	×	×
Franco-German: Gravatt, Marshall and Spaulding	0	21	0	[b]×
Frauendorf: Gravatt	2	2	×	....
"Giant Red": Gravatt and Marshall	8	10	×	×
"Giant White": Gravatt	4	4	×	×
Goliath: Spaulding and Taylor	2	2	×	....
Greenfield: Spaulding and Taylor	2	4	×	....
Holland: Gravatt	0	5	0	[b]×
Imperial: Gravatt	2	2	×	....
"Improved Cherry": Gravatt	6	6	×	××
Knight: Gravatt, Spaulding, and Taylor	5	6	××	....
"Large Red": Spaulding and Merrill	2	3	×	....
"Large White": Gravatt	4	5	××	××
London: Gravatt and Marshall	20	22	[b]×	[b]×
"Marvin Crystal": Rhoads	1	1	×	....
Moore Ruby: Gravatt, Hedgcock, and Marshall	9	10	×	×
New Red Dutch: Spaulding	1	1	×××	....
North Star: Colley and Taylor	0	1	0	××
Norway: Gravatt	5	5	××	××
Palluau: Gravatt, Spaulding and Taylor	5	6	××	××
Perfection: Marshall	1	1	×	×
Raby Castle: Spaulding	2	2	×	....
Red Dutch: Spaulding and Taylor	2	2	×	×
"Red English": Spaulding	1	2	×	....
Red Grape: Gravatt	3	3	×	....

[b] Slight.

TABLE I.—*Results of inoculations made on various species and horticultural varieties of Ribes, etc.*—Continued.

Species or variety and investigators.	Inoculations.		Susceptibility.	
	Infection.	Number.	In the greenhouse.	Out of doors.
SEC. 3.—*Varieties of Ribes vulgare*—Con.				
Redpath:				
Spaulding	0	1	0	....
Rivers:				
Gravatt	4	4	(*d*)	....
Sablons:				
Spaulding and Taylor	1	2	×	....
Scotch:				
Gravatt, Merrill and Spaulding	3	5	×	....
Simcoe King:				
Spaulding	0	1	0	....
Skinner:				
Gravatt	2	2	×	×
Striatum:				
Spaulding	1	1	××	....
Transparent:				
Gravatt	10	10	×	×
Turinoise:				
Gravatt and Taylor	5	5	××	....
Utrecht:				
Gravatt	2	2	×	0
Verrieres:				
Gravatt and Spaulding	4	4	××	....
Versaillaise:				
Gravatt, Marshall and Spaulding	6	7	×	××
Victoria:				
Gravatt, Spaulding and Taylor	6	6	×	×
Warner:				
Gravatt	2	2	×	....
Wentworth:				
Spaulding	1	1	×	....
"Wentworth White":				
Gravatt	2	3	×	....
"White Bar le Duc":				
Marshall	0	1	....	×
"White Brandenburg":				
Spaulding	0	1	0	....
White Champion:				
Gravatt	3	3	×	....
White Cherry:				
Spaulding	1	1	×	....
White Dutch:				
Gravatt and Marshall	4	4	....	×
White Gondouin:				
Gravatt and Marshall	5	5	×	×
White Grape:				
Marshall	11	11	....	×
White Imperial:				
Gravatt, Hedgcock and Taylor	4	5	××	×
"White Kaiser":				
Spaulding	1	1	×	....
"White Leviathan":				
Gravatt and Merrill	5	5	××	....
White Pearl:				
Spaulding	1	1	×	....
White Versailles:				
Merrill and Taylor	1	2	0	....
Wilder:				
Spaulding	2	2	....	×
Wilson:				
Marshall	1	1	....	×
SEC. 4.—*Varieties of Ribes reclinatum.*				
Achilles:				
Spaulding	0	1	0	....
Alma:				
Rhoads and Taylor	1	3	×	....
Berkeley:				
Gravatt and Marshall	5	6	××	×
Carmen:				
Gravatt	5	5	×	×
Carrie:				
Marshall and Taylor	4	5	×	××
Champion:				
Gravatt and Taylor	1	2		....
Chautauqua:				
Spaulding	1	1	×	....
Columbus:				
Spaulding	4	4	....	×
Cumberland:				
Gravatt and Spaulding	2	3	×	....
Downing:				
Gravatt and Spaulding	2	4	0	×
Duncan:				
Merrill and Taylor	2	2	×	....
Golden Prolific:				
Gravatt	6	11	××	××
Houghton:				
Gravatt and Spaulding	2	12	×	×
Industry:				
Gravatt	2	2	×	×
Josselyn:				
Spaulding	0	3	0	×
Keepsake:				
Gravatt	4	6	×	×
Lancashire Lad:				
Gravatt	2	2	×	×
Mabel:				
Spaulding	0	2	0	....
Mountain:				
Gravatt and Spaulding	3	7	×	×
Oregon:				
Gravatt and Taylor	2	7	×	×
Pearl:				
Gravatt and Taylor	5	6	×	××
Poorman:				
Gravatt	2	3	××	×
Portage:				
Gravatt	4	4	×	×
Smith:				
Marshall and Spaulding	3	3	×	×
Transparent:				
Gravatt and Marshall	5	6	×	×
Triumph:				
Gravatt, Hedgcock and Spaulding	9	10	×	×
Van Fleet:				
Gravatt	2	2	×	×
Victoria:				
Gravatt	1	1	×	....
White Lion:				
Marshall	1	1	....	×
Whitesmith:				
Gravatt	2	3	×	×

d Dead spots only.

Recently Thayer (159) and Bunyard (8) have published results of their studies of the cultivated red and white currants. They find these currants to be of mixed and badly confused parentage, but conclude that certain varieties sprang from each of the three species, *Ribes vulgare, R. rubrum,* and *R. petraeum.* Many varieties are still to be assigned to the proper species; hence, they are grouped in Table I under the name *R. vulgare,* for convenience, as it is yet impossible to assign all of them to any species.

The gooseberries are well known to be in many cases a mixture of *Ribes reclinatum* with several American species or even pure selections of American species. For convenience they are grouped under the species name, *R. reclinatum.*

Susceptibility of Ribes Species and Varieties to Cronartium ribicola.

Estimates of the susceptibility of the various species and varieties of Ribes have been made. (See Table I.) These are based on work done in the greenhouse and on results of the experiments out of doors on Block Island. These estimates have been made mostly by two persons, so that they are believed to be quite reliable and accurate by the standards chosen. The estimates for the inside experiments were made entirely independent of those out of doors. The two agree surprisingly. They are based on the results of work covering several years, but many of the species and varieties have been subjected to infection but a single year. A few species will be noted which have remained immune in our tests. But some of these species are known to have become infected elsewhere. This is true of *Ribes alpinum* which is reported to take this disease in Europe, although it is entirely resistant in North America (35, 53). *Ribes innominatum* has been well tested and took the disease only on newly developed leaves. It is a very resistant species. *Ribes sterilis, R. tenue* and *R. villosum* have not yet undergone satisfactory tests, so that no conclusive statement concerning them can be made.

The species of Ribes vary in susceptibility from the extremely susceptible *Ribes nigrum* to the very resistant *R. leptanthum.* On the former are produced the maximum number of uredinia and telia of the largest size, while on the latter the minimum number is produced and these are poorly developed. *Ribes alpinum* has been entirely immune with us, although it takes the disease in Europe.

The varieties of a cultivated species run fairly true to the species as a whole. Some real variation among varieties is believed to depend upon their mixed parentage. Many tests were necessarily made when the plants were not at the most favorable stage of development for the fungus to attack, and it is likely that further tests of aberrant varieties may bring most of them back into agreement with the species to which they belong. Of the varieties of the cultivated red currants which have been tested, the following are nearly immune: Eyath Nova, Franco-German, Holland (see also Tubeuf, 174), London, Rivers, Simcoe King. That is, plants tested under these names have so far shown themselves resistant, but not entirely immune.

The cultivated gooseberries, varieties of *Ribes reclinatum* in some cases more or less mixed with American species of gooseberries, are resistant but occasionally will become infected.

Resistant species and varieties have been found reacting to the fungus and affecting it as follows:

(1) Decreased number of uredinia and telia.
(2) Above accompanied by reduction in size of uredinia and telia with lowered viability.
(3) Small streaks and flecks of dead or dying tissue in infected leaves with uredinia and telia. (See Pl. V, fig. 1.)
(4) Small dead spots formed early with very few or no uredinia and telia. (See Pl. V, figs. 3 and 4.)

This agrees essentially with the results of Stakman (149) with *Puccinia graminis* on resistant grains.

LIFE HISTORY OF CRONARTIUM RIBICOLA.

The Peridermium Stage on Pines.

THE INCUBATION PERIOD ON PINES.

According to European investigators, *Cronartium ribicola* has an indeterminate incubation period between infection of pine and production of æcia. This varies from about two to four years, and possibly much longer. In one of Klebahn's inoculation experiments he got pycnial drops on young white pines 11 months after the inoculation (71). In another instance, infection probably occurred in 1887, pycnia were produced in 1888, and æcia in 1889 (65). Recently Tubeuf (174) reported the results of successful inoculations on *Pinus strobus*. Inoculations were made on September 11, 1914; pycnia formed in July, 1915; they were also produced in 1916 in May and thereafter; æcia appeared in April, 1917.

In North America considerable attention has been given to this matter. McCubbin (84) first attacked it by extensive studies of naturally infected trees. He concluded that five seasons were necessary for most of nearly 1,600 infections in Ontario to develop mature æcia. He outlines the process as follows: first season, infection occurs; second season, dormant; third season, swelling of the bark; fourth season, swelling with pycnia; fifth season, mature æcia. This makes a lapse of about three years and six months between actual infection and the formation of mature æcia.

Stone (153) in 1917 studied this problem in a locality where the fungus was fruiting on white pines for the first time after infection occurred. The infection came from *Ribes cynosbati*, which in 1914 was heavily infected. The Ribes plants were removed in the spring of 1915, so that infection was limited to the season of 1914. Of 40 infections found, 12 were on 1913 wood and produced æcia in May, 1917; 28 were on 1914 wood and produced æcia in May, 1917. The period of incubation for the former cases could not be more than three years and nine months. It may be that infection took place on 1-year-old wood, in which case the incubation period would be only two years and ten months, as was the case with the 28 infections on 1914 wood.

Study of infected branches which had just borne æcia for the first time was made by Posey and Gravatt in 1917 at Stratham, N. H. Their notes show that more than 99 per cent of these infections might be 3 years and 6 months old, but could be no older. In another locality, they found a number of æcia upon growth of the year 1915, making an incubation period of about 18 months.

The first successful inoculations of pines with sporidia of *Cronartium ribicola* are apparently those made by Klebahn on August 27, 1903 (71). *Ribes nigrum* leaves with telia were placed over two young trees of *Pinus strobus* and the whole covered with bell jars as long as the Ribes leaves remained fresh. On June 19, 1904, these trees had swollen twigs bearing juvenile leaves. Early in July, pycnial drops formed, after a lapse of 10 months. It is probable that in the normal course of events æcia would form the next May. This would make an incubation period of about 19 months.

The writer (133) in November, 1910, inoculated a number of healthy *Pinus strobus* trees in the greenhouse with teliospores. These inoculations were made on the young bark. In January, 1912, one each of those inoculated with wound and without wound of bark developed marked swelling. A little later pycnial drops formed, but snails ate them and the surrounding bark, so that the infections did not develop. Apparently it would have been a matter of but a few months when æcia would have formed. This would give an incubation period of about two years. In May, 1916, the writer (145) set out healthy *Pinus strobus* trees among some experimental Ribes bushes on Block Island, R. I. The Ribes were heavily infected the rest of the season. Telia began to form the latter part of July and were abundant by September. On May 10, 1918, several of these trees were found bearing æcia. This makes a maximum incubation period of about 21 months.

In 1917, 10 young plants of *Pinus flexilis* were set out in the experimental plat on Block Island. Nine of them have lived. In the spring of 1920 seven of them bore æcia of *Cronartium ribicola* on the growth of 1918, and the other two were much swollen and discolored, so that if alive they will certainly produce æcia in 1921. It appears that *P. flexilis* is very susceptible. The experiments on Block Island indicate that it is even more susceptible than is *P. strobus*. The incubation period would be about 20 months. A number of *P. strobus* trees set in 1917 also bore æcia in 1920, and many more will do so in 1921.

Clinton and McCormick (12, 15) found that artificially infected trees of *Pinus strobus*, kept in the greenhouse, developed pycnial drops in five to six months after inoculation.

All of the writer's experience in various outbreaks of this parasite shows that most of the newly formed æcia are located on nodes and internodes that are 3 years old or over. It is rather exceptional for æcia to be borne on needle-bearing wood 2 years old, in which case the minimum incubation period is about 18 months. The average incubation period out of doors is approximately 3 years and 6 months.

TIME, PLACE, AND MANNER OF INFECTION OF PINES.

There is constant danger of infection of pines at any time after telia form; that is, after about the 1st of June. The teliospores produce sporidia in 6 hours under favorable conditions.[6] The sporidia germinate immediately. According to Clinton and Miss McCormick, infection of pine leaves may take place within 48 hours (14, 15) after the germinating sporidia are placed on the leaves. Any period of moist weather of 54 hours or longer after about June 1 may cause infection of pines.

The available evidence indicates that infection of pine twigs takes place in or about the bases of the leaf fascicles (71, 84). If this is true for most cases, as seems likely, infection of *Pinus strobus* can occur only on wood that is 1 or 2, or exceptionally, 3 or 4 years old. This follows from the fact that the needles of this species ordinarily live only two seasons, but rather exceptionally they may live three or four seasons.

Tubeuf (174) in 1917 published the results of successful inoculations with sporidia of *Cronartium ribicola* on pines. He inoculated *Pinus strobus, P. lambertiana, P. excelsa, P. parviflora, P. peuce, P. cembroides, P. flexilis, P. montezumae,* and *P. cembra.* He got yellow spots on the needles of *P. lambertiana* but no further results were noted. *P. strobus* became infected readily and bore æcia, but none of the other species showed definite signs of infection. Infection evidently occurred in the needles, many of them having yellow spots. They were also present on the stems. Mycelium was abundant in the yellow areas. Tubeuf says that infection of the stem from the leaves is not common, but that direct infection of the stems is much more likely to occur. No pycnia were obtained on leaves, although the masses of mycelium in the yellow spots seemed to form the base for the pycnial spots in the bark. Older plants of *Pinus strobus* became infected less readily than those only 2 years old. This

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[6] York, H. H. Field studies of Cronartium ribicola in the White Mountains of New Hampshire. Seen in manuscript. To be published in Phytopathology.

infection of young plants he attributes to the fact that shoots bearing primary (juvenile) leaves go into the winter season with buds at all stages of growth, and many are incompletely protected by bud scales. Inoculations made on September 11, 1914, with sporidia succeeded on the primary leaves, on the secondary (mature) leaves, and on the epidermis of growing buds and of young shoots. Yellow spots were present on all these parts in the spring of 1915.

Clinton and Miss McCormick (12, 14, 15) have recently announced successful inoculations in the leaves of *Pinus strobus*. Studies of thousands of infections show that infection takes place through the stomata of the pine leaves of all ages. Inside the stoma a substomatal vesicle is formed which is of a characteristic shape. Thence the mycelium extends into the vascular bundle and then grows rapidly downward to the twig. Infection may take place in 48 hours. Inoculations on stems did not succeed. Inoculations on opened and unopened buds succeeded in a few cases, results being somewhat doubtful with the unopened ones. Infections on the leaves become visible, about a month after inoculation, as tiny yellowish spots centering on the line of stomata on the under side of the leaf. These spots turn golden yellow. Similar yellow spots may form on the twig after the fungus has become established there. A yellow mottling of the infected leaves is the principal symptom of the disease at this time.

This is rarely noted in nature, but two instances having been seen by the writer before 1920 (131, 132, 133, 134). The spots were on both leaves and stems of naturally infected *Pinus strobus* trees. Richards has recently found them on naturally infected leaves. So far as known they have been mentioned previously only by Tubeuf (174); Klebahn (71), who noted them on artificially infected trees but failed to designate the point of infection; and by Pechon (105), who observed them on naturally infected trees. The writer thought the yellow spots resulted from the growth of the fungus outward from the stem into the leaves. Klebahn seems to have been of the same opinion. It is believed that this happens sometimes. In 1920 such spots were seen on pine leaves naturally infected at Temple, N. H., and at New Boston, Mass. They are abundant in certain localities. Artificial infections have resulted from inoculations into the bark of the stem by the writer (133).

Cronartium ribicola is able to grow in bark much more than 3 or 4 years old if it once gains access to the interior. Infections have been seen which were still producing æcia on bark up to 35 years of age. A common method of infection of pine trunks 20 or more years of age is by growth of the mycelium from infected small side branches (135). (Pl. II, figs. 1 and 3.) Very often a twig near the base of a large branch becomes infected. The disease then extends downward into the large branch, and from that into the main trunk of a tree, finally girdling it and killing the entire tree. This is true of nearly all of the older trees that have been killed in North America.

TYPES OF INFECTION ON PINES.

There may be said to be three types of infection on white pines resulting from natural inoculations. These are (1) direct infection of the main trunk on the leader; (2) direct infection of young branches or twigs; and (3) infection of an old trunk by spread of the mycelium from an infected branch. (Pl. II, figs. 1 and 3.) All of these are present in outbreak areas in North America. Direct infection apparently occurs only on growth not more than 3 years old. Infection of large branches or trunks, so far as we can judge, is limited only by the thickness of the bark. Old rough heavy bark of *Pinus strobus* was supposed to be immune to attack, but it has become infected by spread of the mycelium from infected side branches. It is a common method of entry of the fungus into older parts of a tree which were formerly supposed to be too old to become infected. It is very frequent in older outbreaks. This has not been mentioned in European literature until 1918 when Fischer (41) called attention to it.

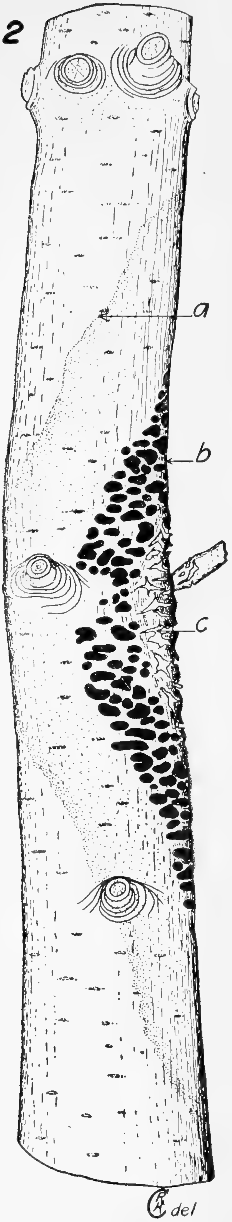
DIAGNOSIS OF BLISTER RUST IN PINE BARK BY MEANS OF THE MYCELIUM.

In 1916, and to some extent before that date, when numerous specimens of diseased white pines were sent to the Office of Investigations in Forest Pathology for quick and reliable diagnosis of the blister rust, many specimens were received which bore no fruiting bodies of the parasite. The appearance of many of these made it practically certain that they were infected with *Cronartium ribicola.* Colley (16, 19) studied the problem and shortly decided that the mycelium and the haustoria did furnish reliable evidence for identifying this parasite in the bark of *Pinus strobus.* The large intercellular hyphæ, the large and abundant haustoria, and their manner of attacking the living cells, were found to be entirely different from the characters of any other known parasite of *Pinus strobus.* The use of these characters for four successive seasons with great numbers of specimens in various stages of development has indicated that such diagnosis of the disease is absolutely reliable.

LONGEVITY OF THE MYCELIUM IN PINE SLASH.

In November and December, 1916, some diseased native white pines were cut in outbreak areas in Ontario and in Maine, the slash being left lying upon the ground. Entirely independent observations made by McCubbin in Ontario and by Posey in Maine early in May, 1917, showed that new æcia were forming abundantly upon

1



2

3

SECTIONS OF PINE TREES, SHOWING TYPICAL PROGRESS OF BLISTER-RUST INFECTION.

FIG. 1.—Section of the trunk of a young tree of *Pinus strobus*, showing entrance of the blister rust into the trunk from an earlier infected branch. The dark shading on the trunk indicates the visibly infected portion. × 1. Drawn by J. M. Shull. FIG. 2.—Trunk of young tree of *Pinus strobus*, about 2 inches in diameter, showing (by zonation) the progress of the blister rust. The disease entered the trunk from the side branch. The cracked bark (*c*) indicates where æcia have formed; the black spots (*b*) indicate the developing pycnia; the shaded part outside (*a*) indicates the area where the bark is discolored. × ½. Drawn by R. H. Colley. FIG. 3.—A trunk 8 to 10 inches in diameter. The disease attacked the swollen twig first, then ran downward to the main branch, from which it has spread into the trunk. The latter will soon be girdled and the tree will die. Photographed by J. F. Collins.

the cankers on this slash (89). This overwintering of the fungus by means of the mycelium is favored by the slash lying in moist places. It was also noted that a piece of a trunk several inches in diameter was producing new æcia after being kept in the dry air of the artificially heated laboratory in Washington about 6 weeks. These findings are significant, since they show that the cutting of diseased pines, if done in the late fall, winter, or early spring, must be accompanied by careful collection and burning of the infected slash, if infection of near-by Ribes is to be prevented. This difficulty may be obviated by cutting the pines in summer when the following hot, dry weather will kill the slash and end the life of the mycelium within it.

SEQUENCE OF PYCNIA AND ÆCIA AND PROGRESS OF THE DISEASE IN PINE BARK.

Study of many blister-rust cankers of varying ages in the bark of large trunks of pine has shown that the disease extends through the bark in a regular and well-defined manner. Cankers of several years' standing usually consist of four distinct zones (20) (Pl. II, fig. 2):

(1) An inner central zone of dead rough bark where æcia have been borne in preceding seasons. This area often has at its center a dead lateral branch or twig down which the disease has traveled from its first place of infection. This is the most common method by which infection of large trunks and branches takes place.

(2) An annual zone of living, swollen bark surrounding the dead area. Here is produced the latest crop of æcia. This zone varies in width from a fraction of an inch up to several inches.

(3) A zone of discolored living bark bearing the pycnial spots, drops, or scars.

(4) An outer zone of living bark, little or not at all swollen, showing a yellowing or bronzing of the normal green color of the smooth living white-pine bark. These zones of course move steadily outward with the progress of the mycelium.

This sequence of zones of activity shows that we have a regular succession of events, as follows:

(1) Invasion of healthy bark by the fungous mycelium, resulting in yellowing and bronzing of the invaded bark.

(2) Formation of pycnia in discolored and often swollen, but still living bark.

(3) Formation of æcia in living bark which has previously borne pyncia.

(4) Death of the bark which has borne æcia in abundance.

Investigations by Gravatt and Posey, and Colley (20, p. 650–651) indicate that the bark is often killed by invading secondary fungi as well as by *Cronartium ribicola* itself. Rhoads,[7] York,[8] and Pennington [9] found that occasional patches of bark, where æcia have been borne the previous year, remain alive and bear a second crop of æcia the second season.

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[7] Rhoads, A. S. Studies on the rate of growth and behavior of the blister rust on white pine in 1918. Seen in manuscript. Published in Phytopathology, v. 10, p. 513–527. 1920.

[8] York, H. H. Op. cit.

[9] Pennington, L. H. Investigations on the white-pine blister rust in New York. Seen in manuscript. To be published as Tech. Bul., N. Y. State Col. Forestry.

Rhoads[10] came to the conclusion that the disease spreads from the original point of infection upward and downward at about equal rates of progress. Posey and Gravatt, and Rhoads found that it spreads at nearly the same rate laterally on both sides. Progress upward and downward is usually more rapid than it is sidewise. It also appeared that in infections not yet bearing æcia, the point of greatest swelling is where infection first took place and where æcia will be first produced. Very often a dead twig or a leaf scar shows very plainly the original point of entrance of the fungus to the bark. Rhoads concluded that infections on shaded lower branches do not spread as rapidly as those on vigorously growing ones, but Posey and Gravatt [11] find that the former are more likely to be attacked by secondary fungi, which soon kill the branches.

Posey and Gravatt [11] found that there are more or less frequent instances in old infected areas of white pines where the infections on lateral branches die out. The statement (131, p. 16; 141, p. 5) that trees once infected with this fungus never recover was largely based upon studies of trunk infections. Like all rules, it has its exceptions, as here indicated. At Kittery Point, Me., Posey and Gravatt studied one of the oldest outbreaks in North America. Trees of all ages from a few years up to 50 or 75 were infected. Here it was found that secondary fungi often kill the blister rust in an infected branch and that increasing suppression of lower branches killed many of the infected ones before the blister rust spread to the trunk of the tree. It was found that about 15 per cent of all the infected trees in the area studied recovered from the disease by the action of these two factors.

THE PYCNIA AND PYCNOSPORES OF CRONARTIUM RIBICOLA.

The pycnospores of the Uredinales have received comparatively little attention, since it has been generally accepted that they are apparently functionless (10, 21, 70, 110, 122, 155). The writer can find but little data upon which this idea is based. Plowright (110), Thaxter (158), Jaczewski (47), and Klebahn (68) are the only investigators known to the writer who have actually inoculated plants with the pycnospores of their rusts. It seems that the pycnospores should be more thoroughly tested.

The work with pycnospores of *Cronartium ribicola* in Europe seems to be limited to that of Klebahn (68), who made inoculations with them upon young *Pinus strobus* trees without infection occurring. Even in this case there was not a clear-cut result, such as is to be desired. More recently Colley (18) has shown the importance of the pycnial spots, drops, and scars as symptoms of the blister rust in pine bark, and still more recently (20) he has investigated their morphology and cytology.

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[10] Rhoads, A. S. Op. cit.

[11] Posey, G. B., and Gravatt, G. F. Field studies on the white-pine blister rust at Kittery Point, Me. Seen in manuscript.

GERMINATION OF THE PYCNOSPORES.

Plowright states that pycnospores (spermatia) of some of the Uredinales have been germinated in sugar solutions by Cornu and himself (110). Brefeld (7) states that the spermatia of several rusts have been germinated in culture solutions. Later Carleton (10) stated that he had been able to germinate the pycnospores (spermatia) in but a single instance.

> The spermatia of *Uredo caeoma-nitens* Schwein., budded sparingly on May 31, 1893, after 24 hours in a dilute solution of honey, but would not germinate in water.

Still later he said (11):

> Until recent years it was not supposed that the spermatia produced regular germ tubes, but that the germination is always simply a process of budding. Dr. N. A. Cobb and the writer have shown, however, that ordinary germ tubes are produced in the germination of these spores as well as in the other spore forms * * *. Spermatia, though germinating readily in water, will be found to do much better in a rather dilute sugar solution, or perhaps still better in a solution of honey.

Investigations were made in 1918 by York and Overholts,[12] who tested their germination in water and in various solutions of glucose, cane sugar, dextrose, maltose, lactose, peptone, extract of macerated Ribes leaves, and extract of macerated pine bark. Fresh pycnospores gave no germination. Pycnospores subjected to the cold of an ordinary refrigerator from 3 to 20 days gave degrees of germination increasing with the length of time in cold up to 18 days. Germination occurred in 3, 5, and 6 per cent cane sugar and in 3, 6, and 10 per cent dextrose. The stronger dextrose solutions gave the best results. No germination occurred in tap water in any case.

SEASON OF PRODUCTION OF PYCNIAL SPOTS, DROPS, AND SCARS.

The dark spots (Pl. II, fig. 2, *b*) which precede the exudation of the pycnial drops may be found in the infected bark at all times of the year. Records and observations made from 1909 to date furnish definite data on the season of pycnial drop formation. (See Table V, p. 72.) The pycnial drops are produced immediately after the æcial season; that is, from about June 20 until winter. The rusty-brown scars left after the disappearance of the drops may be seen at all times of the year on old cankers. On new infections the scars, of course, do not appear until the drops have formed and disappeared. All of these are positive symptoms of this disease in white pines.

THE ÆCIA AND ÆCIOSPORES OF CRONARTIUM RIBICOLA.

SEASON OF PRODUCTION OF THE ÆCIA.

The æcia develop at varying dates in the same locality in different years, according to the season. The locality, whether a warm or cold exposure, at a low elevation or a high one, well to the south or

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[12] York, H. H., and Overholts, L. O. The germination of the pycnospores of Cronartium ribicola. Seen in manuscript. To be published in Phytopathology.

far north, has much to do with the time that the æcia appear. They begin to push through the bark several weeks before they break open and distribute the æciospores. Open blisters have been noted as early as April 5 in eastern Massachusetts, but they were nearly three weeks later in the Adirondacks the same spring. Table V (p. 72) gives specific data so far as they are available for this and related dates.

Klebahn (68) stated that æciospores are produced by an æcium of *Cronartium ribicola* for more than 14 days. Posey and Gravatt [13] found that æciospore production took place at Kittery Point, Me., in 1917, from April 29 to July 1.

In the spring of 1918, Rhoads made observations at Kittery Point, Me., to determine how long individual æcia produce spores.[14] On May 3, he stuck pins, bearing numbered pieces of paper, into 300 æcia on various trees just as they first broke open. On May 20, the peridia of all but 63 of the æcia were entirely gone with most of the spores. On May 29 remnants of but 19 were left and on June 4, none. Therefore, in 1918 the æciospore season was about 4 weeks long at Kittery Point, Me.

York [15] working at North Conway, N. H., in 1918, found that a few individual æcia contain viable spores for from 20 to about 30 days. A study of æcial production on single cankers showed that æcia matured for a period of about 30 days. These infections were all on relatively small twigs and branches. On larger branches or trunks the period may be longer. Study of the period of æcial production in that entire region showed that it was approximately 70 days. At Lewis, N. Y.,[16] the æcial season in 1919 was slightly more than two months in length. After the main æcial season, late straggling æcia form. Rhoads [14] noted that æcia occasionally develop on areas of bark which bore æcia the preceding year, but which were still alive.

York noted a newly formed æcium of *Cronartium ribicola* near Littleton, N. H., on July 21, 1918 (179). Several still more remarkable cases were noted by York and Ninman at Amery, Wis., on September 15 and 16, 1919. Such late æcia appear to be unknown for any of the other stem Peridermiums except *C. occidentale*, which has an æcial season from June to August. Numerous instances are known where *C. ribicola* was entirely absent on Ribes in a given locality early in the season, but later was found to be present in greater or less abundance. Some of these infections may originate from such late æcia. These late æciospores may remain viable over winter in the æcia, since Dosdall (29) has found that æciospores occasionally retain viability until the next spring.

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[13] Posey, G. B., and Gravatt, G. F. Op. cit.

[14] Rhoads, A. S. Op. cit.

[15] York, H. H. Op. cit.

[16] Pennington, L. H. Op. cit.

Observations by Pennington[17] on the æcia showed that more æcia were produced per canker and many new cankers were fruiting in 1919, so that more æciospores were produced that year than in 1918 in the Adirondacks. Observations on the first generation of uredinia and the results of spore-trap work indicated, however, that not as many æciospores were set free in 1919 as in 1918. This is supposed to have been due to heavy rains, which beat them down from the air. The distribution of the first generation of uredinia showed that the æciospores were as widely disseminated in 1919 as in 1918.

DISTANCE OF DISSEMINATION OF THE ÆCIOSPORES.

As is true of many of the more difficult points in the life history of *Cronartium ribicola*, European statements concerning the distance that the æciospores are distributed are based apparently mostly on personal opinions. The value to be attached to these statements seems to rest on the known excellence, or the reverse, of the published work and judgment of the writer who is being considered. European mycologists have mentioned a number of instances where this fungus appeared on Ribes which were said to be far removed from white pines. But some of these cases were later found to be actually much nearer diseased white pines than was at first supposed. Tubeuf (166) has stated that the æciospores spread the disease up to 500 meters or more. On the other hand, a considerable number of definite recommendations for separation of the alternate hosts set a distance of only 30 to 100 meters (131, p. 41–42).

In North America earlier field experience indicated that the æciospores spread the disease for rather short distances from their source. It was recognized from the beginning that these spores are exceedingly light and well adapted to wind dispersal, and it was stated that our knowledge of their dispersal was very limited. Special efforts have been made for three seasons to gather more data on this problem.

Posey, in 1917, set bushes of *Ribes nigrum* in a salt marsh at Kittery Point, Me., at varying distances from infected pines before uredinia were formed. Some infection resulted from æciospores upon Ribes plants more than a quarter of a mile from any white-pine trees. The infecting spores probably traversed several hundred yards additional, as the nearest pines were not known to be diseased. The heavily infected area was about 1¼ miles distant, and the infecting spores may easily have come that distance.

Posey also examined the islands of the Isles of Shoals, off Portsmouth, N. H., for the presence of *Cronartium ribicola*. He found no pines, but a number of *Ribes hirtellum* plants. A few leaves were

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[17] Pennington, L. H. Op. cit.

found infected with the fungus. In 1920, Snell reexamined these islands much more carefully. He again found the fungus on several leaves and decided that it is evidently a case where the æciospores were blown from infected pines to the islands. The islands are about 7 miles from the mainland, so that it appears that the æciospores may be blown this distance and infect Ribes. There appeared to be no reason for thinking the fungus wintered over. At any rate, it must have come from the mainland originally. The islands where the disease was found are very seldom visited, so carriage of spores in this way appears to be eliminated.

McCubbin (88) found that the æciospores fall about 8 feet in seven minutes in still air. This indicates a very wide potential distribution of these spores by a moderate breeze.

In 1918, York and Overholts (cited in Spaulding, 145) worked in the White Mountains of New Hampshire in a generally infected region. Much work was done with spore traps and much time spent in examination of Ribes plants which were isolated from white pines. The work proved that the æciospores are distributed for miles to the tops of adjacent mountains approximately 3,000 feet high, that they arrive in a viable condition, and that they are the means by which the disease spreads far and wide to Ribes.

In 1918, also, Pennington and Snell (cited in Spaulding, 145) worked in the eastern Adirondack region of New York. Spore traps here gave valuable contributory evidence, but study of the distribution of the first generation of urediniospores with reference to neighboring white pines gave the best results. Here it was found that spore traps caught æciospores up to 550 feet from any pines. Within a large area of cultivated land at Essex, N. Y., an intensive study was made by Snell (128) of the first generation of urediniospores. In this area the Ribes were found to have first-generation uredinia sparingly and widely scattered; that is, the æciospores causing the infection evidently came from a considerable distance. In one case diseased Ribes were found three-fourths of a mile from any white pine. Several others were found at smaller distances from any pine trees. It was concluded that the æciospores came from a distance of not less than three-fourths of a mile and probably much farther.

These conclusions concerning the wide spread of æciospores in the two localities were arrived at independently and without the knowledge by either party of what conclusions had been reached by the other.

In 1919, Snell (128) found near Rush Lake, Minn., infections on Ribes leaves which were 1¼ miles from the nearest pine and about 3 miles from the nearest known diseased pine. Many such infections were found in the same general area which were half a mile or more from any pine. These infections were found developing when the first generation of uredinia appeared throughout that general infected area. They must have been produced by æciospores which had been blown at least the above distances.

In 1919, York caught and germinated æciospores on the summits of two mountains nearly 4,300 feet above the adjoining lowlands. It is evident that altitudes such as this do not prevent the spread of this fungus. Pennington [18] caught æciospores up to 1,200 feet distant from pines and found diseased Ribes three-fourths of a mile from any pine tree.

AGENTS DISSEMINATING THE ÆCIOSPORES.

It has been evident from the beginning that wind is a most efficient and active agent in the distribution of the spores of *Cronartium ribicola.* While the probability of spore carriage by other agents such as insects and the larger animals was recognized, no time could be spared for work upon it. More recently, Gravatt and Marshall (45) and Gravatt and Posey (46) have made some studies of this sort.

Gravatt and Marshall worked in the experimental greenhouse where no æcia were present. They found that pycnia and the surrounding bark tissues were eaten by sow bugs.

Gravatt and Posey (46) made studies in the field in a heavily infected pine area at Kittery Point, Me. Here it was found that gipsy-moth larvæ, which were abundant, fed eagerly on the pycnia and æcia of the blister rust and also ate the bark tissues immediately adjacent to them. It was found that in some cankers a considerable percentage of the fruiting æcia were thus destroyed. But a few ingested spores remained viable, as tests in hanging drop cells in tap water yielded a few germinations. These larvæ also were carriers of abundant æciospores on their bodies, many being of a decided yellow color from the spores with which they were dusted. The gipsy-moth larvæ are known to have been blown 20 miles or more. Within the gipsy-moth infested area these larvæ are then dangerous agents in the distant spread of the disease, a fact not previously appreciated.

Notes made by Gravatt show that a wood mouse caught in the outbreak area at Kittery Point, Me., carried a small number of æciospores on its body. While squirrels, other animals, and birds have not been examined, there can be no doubt that they are active carriers of the spores. It is known that the æciospores become attached readily to clothing, and there can be no doubt that persons may carry the disease, at least locally, in this manner.

In a number of outbreak areas where pine infections were just about to produce pycnia for the first time, it was noted by several observers [19]

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[18] Pennington, L. H. Op. cit.

[19] Rhoads, A. S. Op. cit.

(143, 144) that squirrels ate the swollen bark from the infected parts of the branches. (Pl. III.) They undoubtedly run over fruiting cankers and pick up æciospores on their fur and feet. Porcupines may act in the same manner. Birds undoubtedly carry these spores to some extent, and as in the æcial season they begin nesting and largely remain in the same locality they, too, act only as local carriers.

Some indications have been noted where a road traverses a narrow valley, or a narrow clearing in a forest, that automobiles create drafts which carry spores to some distance along the highway. It seems entirely possible for steam trains and electric cars to do the same thing.

POSSIBLE AUTŒCISM OF THE ÆCIOSPORES.

The possible autœcism of the æciospores of *Cronartium ribicola* has been considered. As early as 1913 field observations were made with this point in view, but no evidence of the spread of the fungus directly from pine to pine was found.

The question whether æciospores of other stem-inhabiting pine Peridermiums are capable of infecting pines has received considerable attention. In 1907 Liro (82) stated that he had made 169 inoculations of *Pinus sylvestris* with æciospores of *Peridermium pini* from the same host. No infections resulted. In 1914 Haack (48) stated that he had made similar inoculations and obtained abundant infections. His experiments were performed out of doors, with no protection from natural infection and with trees which already were naturally infected; hence, his results are worthless. In 1913 Meinecke (95) made successful inoculations with æciospores of "*Peridermium harknessii*" upon *Pinus radiata* under controlled conditions. Later (96) he changed the name of the fungus to *Peridermium cerebrum* and reported that he had successfully inoculated *Pinus radiata* with æciospores from *P. radiata* and from *P. attenuata;* and *P. muricata* with æciospores of *P. cerebrum* from *P. radiata.*

In 1915 Hedgcock (51) successfully inoculated trees of *Pinus ponderosa* var. *scopulorum, P. contorta, P. sabiniana, P. caribaea, P. mariana, P. pinea,* and *P. halepensis* with æciospores of "*Peridermium harknessii*" from *P. contorta.* He has also successfully inoculated *P. ponderosa* and *P. virginiana* with æciospores of "*P. harknessii*" from *P. ponderosa.*

In 1918 Klebahn (73) published the results of successful inoculations made by him with æciospores of *Peridermium pini* upon young twigs of *Pinus sylvestris,* both with and without wounds, under controlled conditions. These results throw doubt on the strict heterœcism of the æciospores of all the stem-inhabiting pine Peridermiums.

The following tests have been made with the æciospores of *Cronartium ribicola:* Klebahn (68, 70) repeatedly inoculated young

TRUNK AND BRANCHES OF PINUS STROBUS, SHOWING BARK INFECTIONS OF BLISTER RUST EATEN BY SQUIRRELS.

Photographed by W. H. Snell.

FIG. 1.—An infected branch which was evidently a young infection that had not yet formed æcia. FIG. 2.—Infected bark of living tree. Here may be seen the blister-bearing central area at the base of the branches in place, while the outer, surrounding, pycnial zone has been eaten away. FIG. 3.—Infected bark of living tree. The eaten parts were where pycnia were forming.

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LEAVES OF RIBES INFECTED WITH CRONARTIUM RIBICOLA, SHOWING DIFFERENT TYPES OF ATTACK.

FIG. 1.—Lower surface of a leaf of *Ribes aureum* infected by *Cronartium ribicola*. Note the characteristic isolated infected areas, with the abundant uredinia closely crowded together. FIG. 2.—A Ribes bud with a single leaf which bears normal uredinia. This leaf is relatively old, being stunted in growth by adverse conditions which have held it stationary for several weeks. FIG. 3—Lower surface of an infected leaf of *Ribes vulgare*, horticultural variety White Transparent. Note the large infected areas merging into a single one. The uredinia are not so closely crowded together as in figure 1. FIG. 4.—Lower surface of an infected leaf of *Ribes nigrum*. Note the general distribution of the telia, their grouping closely together, and their vigor of growth.

Pinus strobus trees with æciospores, but without producing infection. Hennings (53) inoculated *P. strobus* trees with æciospores and also with teliospores. No infection resulted from either. In the spring of 1916 the writer made 100 inoculations with wounds into the bark of *Pinus strobus* trees, out of doors, with fresh æciospores of *Cronartium ribicola.* No infections have resulted to date. In May, 1917, the writer (146) inoculated white pines by dipping the tips of young twigs in water containing great quantities of newly formed æciospores of *C. ribicola.* The needles as well as the twigs were covered with spores. Glassine bags, containing wet wads of cotton, were then tied over the inoculated twigs to keep up the humidity of the air. No evidence of infection is yet visible.

GERMINATION OF THE ÆCIOSPORES.

Experience shows that fresh æciospores taken from æcia just as they are about to break open, or just at the time of breaking, possess maximum infective power. Doran (28) confirms this opinion. Inoculations made with such spores are sure of results if conditions are at all favorable. Older æciospores are erratic in germination, but some of them retain viability to a marked degree. Cooling on ice stimulates their germination to a decided degree, as is shown by experiments performed by Eriksson (32), Gravatt, and others. Each spore produces from one to five (20, 29) germ tubes, which branch freely. The viability of fresh æciospores is generally high, as many as 95 per cent germinating under favorable conditions. They require 8 to 10 hours to germinate (28).

Doran (28) determined the minimum, optimum, and maximum temperatures for the æciospores of *Cronartium ribicola.* Five series of tests were made. It was found that germination in distilled-water drop cultures occurred through a range of 12° C., but the percentage of germination dropped rapidly both above and below the optimum. The minimum temperature for the æciospores was 5° C., the optimum was 12° C., and the maximum was 19° C.

LONGEVITY OF THE ÆCIOSPORES.

Klebahn (70, p. 26) seems to have been the only European investigator who has tested the longevity of æciospores. He found them strongly viable after seven weeks.

From the beginning of the work of the writer on *Cronartium ribicola* it has been known that the æciospores retain their viability for a relatively long time under favorable conditions. In 1910 a single æciospore which had been kept in the laboratory for more than five months in an open æcium on a diseased young tree which was dried and kept as a specimen germinated in water (131, p. 30). In 1915 McCubbin (85) collected on May 6 a diseased young white pine bearing æcia. It was placed in a box in the laboratory and allowed to dry out. Tests were made by inoculating leaves of *Ribes nigrum* plants on May 7, May 21, June 4, and June 23. On the last date no infection occurred. In 1916, McCubbin repeated these experiments and found that the æciospores remained capable of infection under the conditions of his experiment at least 39 days. He believes they may retain viability considerably longer, as his tests were conducted under adverse conditions.

Æciospores collected on April 9, 1917, and kept in a closed glass vial were tested by Gravatt weekly in hanging drops of distilled water. They gave good germination for about one month, then weakened until June 9, when the last germination occurred. The tests continued until July 14. On May 7, 1917, another series of similar tests was started by Gravatt and Taylor. (See Table II.) The æciospores were placed in two glass vials with cheesecloth tied over the tops. One vial (B) was kept out of doors on a window sill on the north side of a building where the sun did not shine. The other vial (A) was kept in a dark refrigerator. The spores were tested weekly in distilled water. In most cases the cultures were placed in an ice box for about 12 hours. The spores kept in the ice box retained their color throughout, while those on the window sill had faded perceptibly by June 16. Lot A varied in germination from 8 per cent at first to 3 per cent on June 2. Germination persisted until July 2, when the last occurred in this lot. Lot B germinated freely until May 26 and not at all after June 23. Cooling and darkness in this case decidedly stimulated germination for one month and prolonged viability about 10 days after the uncooled æciospores which were exposed to light had lost all viability.

TABLE II.—*Longevity of the spores of Cronartium ribicola.*

Date, 1917.	Germination (per cent).						Notes.
	Lot A, vial in refrigerator.			Lot B, vial out of doors.			
	Æciospores.	Urediniospores.	Teliospores.	Æciospores.	Urediniospores.	Teliospores.	
May 8.	8	13	90	8	8	85	
May 12.	8	10	85	1	10	90	
May 19.	5	60	80	2	40	85	
May 26.	4	45	70	3	37	50	Not cooled in refrigerator before germination.
June 2.	3	6	40	.8	.8	10	Do.
June 9.	1	.65	51.3	.1	1.5	4.4	
June 16.	.1	1.35	4.5	0	0	0	Lot A somewhat faded.
June 23.	0	0	3.5	.05	0	0	Lot A much faded.
July 2.	.05	0	.5	0	.1	....	Teliospores in lot A mouldy.
July 7.	0	0	0	0	0	....	
July 14.	0	0	0	0	0	....	Æciospores and urediniospores mouldy in lot A, color of lot B still fairly good.

In April, 1918, Dosdall tested in distilled water (in hanging-drop cultures) the viability of æciospores produced in 1917 (29). On April 19, 1918, a dead white-pine branch bearing a canker which had fruited in 1917 was collected at Rush Lake, Minn. While new æcia were just beginning to break open on other cankers at this time, the spores tested were not new ones, as they were dug from the bottoms of 1917 cavities after scraping off the outer exposed spores. Nor could there have been new æcia pushing up beneath the old ones, as the branch was dead. It was found that from 1 to 2 per cent of the spores germinated in distilled water, each spore producing from 3 to 5 germ tubes. It is barely possible that these spores were from an abnormally late æcium (179) and therefore were not so old as Dosdall supposed them to be. Even so, they must have been approximately 6 months old.

This experiment of Dosdall has been repeated. A dead branch bearing æcia of 1918 was collected at Kittery Point, Me., on February 25, 1919, and taken to Washington, D. C. Taylor tested the æciospores by hanging-drop cultures in tap water, but no germination of the spores could be demonstrated. Spores of other fungi were present and did germinate.

York[20] collected a specimen of diseased white pine bearing newly formed æcia on April 30, 1918. This was put in a paper bag and left in the laboratory away from direct sunlight until October 5, 1918. He then broke open a still unbroken æcium which had not pushed through the outer bark and made cultures of the spores. He got some germination in tap water under these condition 157 days after collection of the material. The spores were still yellow when the test was made. Spores from æcia which had broken open did not germinate.

During the season of 1918, Pennington[21] found that in the Adirondacks the æciospores remained viable for at least four weeks after being removed from the æcia and stored in a dry place. The same season, York found that in the White Mountains æciospores from blisters in cankers cut from the tree and kept in the shade out of doors remained viable for 75 days, as shown by tap-water cultures and inoculations on Ribes leaves.

In 1919, Pennington[21] found that æciospores, whether brought into the laboratory or left in the field soon lost their viability, less than 1 in 400 germinating after three weeks from the breaking open of the æcium producing them. Tests upon the viability of æciospores after they had been exposed to direct sunlight showed a decrease of 50 to 75 per cent in viability after three hours' exposure. After an exposure of eight hours, some of the æciospores (1 in 1,500 or 2,000) were still viable.

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[20] York, H. H. Op. cit.

[21] Pennington, L. H. Op. cit.

Doran (28), in 1919, found that the æciospores germinate well in distilled-water drop cultures for four weeks, when germination weakens. Germination ceased after six weeks. He does not give details of the conditions of storage of the spores.

Pennington [22] compared the number of æciospores caught in spore traps with the number of infections on Ribes leaves and estimated that under the most favorable conditions 1 spore in every 25 which lodged upon a Ribes leaf produced infection there. An estimate for the season showed that not more than 1 in 100 produced infection.

The Cronartium Stage on Ribes.

THE INCUBATION PERIOD ON RIBES.

The length of the incubation period between infection of Ribes by æciospores and urediniospores of *Cronartium ribicola* and the production of mature uredinia or telia varies greatly, according to the external conditions of temperature and moisture and the age and condition of the leaves infected. Examination of the records of 493 inoculation tests made in the greenhouse show that the shortest incubation period between infection and formation of mature uredinia is practically 7 days. These records show that 2.4 per cent of the cases fruited in 7 days, a like number in 8 days, 7.3 per cent in 9 days, 10.4 per cent in 10 days, 20.8 per cent in 11 days, and 19.7 per cent in 12 days. The percentage rapidly drops after this to 9.7 per cent in 13 days, 8.1 per cent in 14 days, 8.5 per cent in 15 days, 8.1 per cent in 16 days, and 3.2 per cent in 17 days.

Pennington [22] found that the incubation period on Ribes in the eastern Adirondack region with both æciospores and urediniospores was 11 to 18 days; it was usually 13 to 15 in mature leaves and somewhat longer in leaves which were very young when inoculated.

There are times when the fungus produces only uredinia in the greenhouse as well as in the fields. The behavior of the fungus is not entirely controlled by weather conditions, but is greatly influenced by the condition of the host leaves. At other times the fungus will produce nothing but telia. At such times telia are produced in a very short time after infection. Telia have been obtained in 9 or 10 days after infection. From 12 days upward they may be formed at almost any time up to 2 or 3 months after infection.

York [23] in many cases has obtained telia directly from æciospore as well as urediniospore inoculations upon overmature [24] leaves.

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[22] Pennington, L. H. Op. cit.

[23] York, H. H. Op. cit.

[24] The term "overmature" is here used to denote that stage of development of Ribes leaves where they have become tough, leathery in texture, and of maximum thickness, but have not begun to decline in photosynthetic activity.

METHODS OF INOCULATING RIBES.

The methods of inoculating Ribes plants are not claimed to be original with the writer or his associates. It is well known that some of these methods have been in use for many years. They are given here to show the conditions under which the experimental work was done, as follows:

(1) When plenty of spore material is available, as is usually the case with æciospores, the spores may be placed in a considerable quantity of water and the top or branch of the Ribes plant dipped into it. The spores will be distributed quite evenly over all parts of the dipped plant. (See Clinton (12).) This method was used by the writer as early as 1909, and has been very successful. It uses up large quantities of inoculum, however.

(2) Another method which has been much used is to spray water from an atomizer upon the part to be inoculated, then shake the dry spores upon the wet surface. This also requires a plentiful supply of inoculum. It has been a favorite method, as it gives good results with reasonable certainty.

(3) When inoculating with urediniospores from fresh leaves, the part to be inoculated is sprayed, and the leaf bearing the inoculum is turned with its lower surface on that of the healthy leaf and the two rubbed lightly together.

(4) If the inoculum is scanty, the spores are moistened with a drop of water and lightly scraped off upon the moistened healthy leaf with a sterilized scalpel or knife blade.

(5) If the inoculum is in moderate quantity, the spores are placed in a small quantity of water in a sterilized atomizer and sprayed upon the healthy plant.

(6) The spores, if fairly plentiful, are sometimes collected in a watch glass, a small quantity of water added, and then a clean camel's-hair brush is dipped into the mixture and brushed over the surface to be inoculated. With this method it is advisable to wet the inoculated part with an atomizer after inoculation, or results will be meager.

(7) Occasionally healthy leaves have been rubbed or dipped in the spore mixture described in paragraph 6.

Gravatt made comparative tests of some of the foregoing methods of applying the inoculum. This comparison showed one-fourth more infection with method 5 than with method 6, with three different species of Ribes. General experience has shown the order of efficiency of the methods to be as follows: 1, 5, 2, 6, 3, 7, 4. This is probably largely due to the greater number of spores used by the more successful methods. All will give good results when the relative number of spores used is considered.

With all these different methods of applying spores and moisture, it is essential to supply all the water possible without having it form large drops and run off.

As a supplement to the local moistening, it is necessary to keep the inoculated plant in a moist chamber for 12 to 24 hours. In the experiments by the writer and his associates the preferred method has been to keep the plant in the moist chamber 48 hours.

The matter of a proper moist chamber is a problem of considerable moment. Glass bell jars are good, but costly and easily broken. A tightly closed wooden and glass chamber of considerable size was tried, but is unsatisfactory because the tender leaves of the inoculated plants are liable to scald in hot weather. Hunt (57) tested a form of the iceless refrigerator for this purpose. This is a modification of the field moist chamber described by Keitt (61, p. 540–541), without a continuous water spray. It is essentially a framework large enough to receive several potted plants, on top of which a large pan of water is placed. Around the framework is fitted a loose curtain of heavy cheesecloth completely surrounding the framework on the sides and extending from the water in the pan on top to the ground. In use, the cloth is wet thoroughly and the water in the pan keeps it wet. This keeps the air within the chamber saturated with moisture and cool, which is the desired condition for the plant. This has been very successful even in the hottest summer weather and has the desirable qualities of durability, cheapness, portability, and simplicity.

Clinton (12) has recently reported the successful inoculation of plucked leaves of Ribes in moist chambers. This is an old method with the rusts, and was used by Barclay in India as early as 1887 (4). Clinton has apparently developed this method to a point of maximum efficiency. It has not been used in the investigations by the writer and his associates, the preferred method being to retain natural conditions as far as possible in making susceptibility tests.

FACTORS CONTROLLING THE INFECTION OF RIBES.

Among the factors controlling infection of Ribes by *Cronartium ribicola* may be mentioned moisture, sunlight, age of leaves inoculated, and age of inoculum.

Frequent allusions are made by investigators to the need for abundant moisture in producing the infection of Ribes by æciospores and urediniospores of *Cronartium ribicola* and in spreading the fungus on Ribes.

In 1904, Aderhold (1) performed a series of experiments to determine the influence of moisture upon the infection of *Ribes vulgare* by æciospores of *Cronartium ribicola*. He had two inclosed cells, the air in one of which was moistened by artificial rain, while in the other it was kept relatively dry; he had similarly arranged plats open to the free air. The conditions in these cells and plats he summarized, as in Table III.

TABLE III.—*Conditions in cells and plats of Aderhold's experiments.*

Experiment.	Air.	Temperature.	Moisture.	Amount of light.
1. Rain cell	Motionless	High	Very great	Small.
2. Dry cell	do	Very high	Slight	Do.
3. Open rain plat	Moving	Below normal	Great	Great.
4. Open dry plat	do	Normal	Normal	Do.

Aderhold placed his experimental plants in these cells and plats on April 16. On May 6 all of the plants were heavily dusted with æciospores, and half of those in each cell and plat were put under conditions opposite to those they were in before inoculation. The plants from the closed rain cell when inoculated and replaced in the same cell took the disease heavily. Those from the closed dry cell when inoculated and placed in the closed rain cell also took the disease heavily. Those transferred from both the rain and dry cells to the dry after inoculation showed no infection. All the plants kept in the open plats failed to take the disease. It is apparent from his results that infection depends upon an atmosphere that is nearly saturated with moisture.

Experience in the greenhouse has shown that it is necessary to have abundant moisture on the leaf surface for infection to succeed. The leaf itself must be wet, without having large drops of water collect. This moisture must be retained for some time by keeping the surrounding air saturated with water vapor. Gravatt made a series of parallel tests, part of the inoculated plants being kept under bell jars 2 hours, part of them 7 hours, and another part 24 hours. Infection occurred with the 7-hour and the 24-hour plants, but not with the 2-hour tests. The writer made a series of inoculations in the greenhouse with æciospores without putting the plants in moist chambers. Not one infection resulted within 14 days, the usual time necessary to reach full fruiting condition. The plants were then put into moist chambers for 48 hours, and fair infection resulted from the spores put on the leaves 14 days before. Ewert (37) performed a similar experiment in 1912 with the same results, as did Werth (177) in 1915 and York[25] in 1919. McCubbin in 1916 inoculated two leaves on each of seven shoots of a *Ribes nigrum* plant. Two of the shoots were put in a moist chamber for 48 hours. The remaining five shoots were left uncovered. The leaves of only the two inclosed shoots developed infection.

It is equally necessary to have plentiful moisture for infection to occur out of doors. Hennings (53) found a severe outbreak of the disease on Ribes during a dry time in the Dahlem Botanical Garden, but he attributes the intensity of the attack to the daily watering (sprinkling) of the bushes. Ewert (35) says, "In the summer of 1902, moisture, the important factor for infection, was not lacking, so all conditions were favorable for the spread of the Cronartium." Schellenberg (123) attempted to inoculate Ribes bushes with æciospores from *Pinus cembra* in the open air. He attributes his failure to produce infections to the bright sunny weather prevailing at the time. In 1910, the writer (131) inoculated Ribes leaves with fresh

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[25] York, H. H. Op. cit.

æciospores out of doors. The leaves were not wet, but there was dew every night. No infection resulted.

In 1913, Stewart and Rankin (151) made some observations on this problem. On May 14 two white-pine trees were found bearing abundant open æcia. On May 17, they were cut down and burned. About 120 feet from the pines there was a small plantation of *Ribes nigrum* and *R. vulgare*. The weather was dry and unfavorable for infection of the currants to take place for several days before May 15. The forenoon of May 15 was damp, but in the afternoon it dried off and remained dry until after the trees were destroyed. They concluded that the infection of Ribes which developed on June 10 apparently could have taken place only in the wet forenoon of May 15. It appears to the writer that the long incubation period indicates that the spores from the pines stuck to the Ribes leaves without germinating until a later rainy period long enough for infection to occur.

Studies made by Pennington[26] and Snell (145) in New York in 1918 on *Ribes rotundifolium* show the absolute dependence of the spread of this fungus upon moist weather. They found that six distinct generations of urediniospores were produced during the season, with a slight seventh one the last of the summer. These appeared approximately two weeks after spells of rainy weather. York working in the White Mountain region for three years has made a great many successful field inoculations on various species of Ribes without using any form of moist chamber. His work was largely carried on, however, in localities naturally moist.

Temperature also is an important factor. Probably much of the efficiency of Hunt's iceless refrigerator inoculating chamber is due to the rather low temperature obtained. *Cronartium ribicola* is favored by low temperatures, as is shown by the optimum temperatures determined for it by Doran (28). Doran also inoculated plants of Ribes which were then kept at 3°, 12°, and about 22° C. No infection occurred on the first and last, while the one at 12° C. developed uredinia.

Sunshine is an important factor, indirectly if not directly. Its direct influence upon the spores is destructive (30, 88) but it is doubtful if this action is powerful enough to hinder germination greatly if sufficient moisture is present. Indirectly sunshine affects infection by quickly reducing moisture. It seems that a moderately cool temperature is most favorable and that bright sunlight may elevate the temperature above the optimum for the fungus.

The size of the leaves alone seems to have little or no influence upon their susceptibility to infection (147). Leaves as small as

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[26] Pennington, L. H. Op. cit.

4 mm. wide have been found bearing groups of uredinia (Pl. IV, fig. 2).

The age and relative maturity of the leaf has much to do with its susceptibility. It has been the general experience that Ribes leaves may be overmature and also may be too young to take the disease. Infection does not occur on the leaves of a given species of Ribes until they have reached a certain degree of maturity. Leaves produced by buds developing in late summer or fall, even if very small, readily become infected. The different species of Ribes vary much in this regard. *Ribes nigrum* shows a great range in its age of susceptibility, while resistant species become infected only on leaves of a certain maturity. The most favorable stage of growth seems to be about when the leaf attains full size but has not become hardened and leathery as it does later. Tests were made by Gravatt in 1915 in the greenhouse on *Ribus nigrum.* The plant had three shoots of nearly equal size and development. They bore fully mature leaves at the base and had leaves at the tips about half grown. In this case all the leaves became infected except the lower three or four on each shoot. In 1916, McCubbin (ms. report) made several series of inoculations with æciospores upon *Ribes nigrum* leaves of various ages. The plants were not kept under the best growing conditions, so the results are less pronounced than might otherwise be expected. He produced no infection on the youngest leaves. The older ones took the disease, but the overmature ones took it least of all. York[27] made greenhouse tests with plants of *Ribes nigrum, R. triste, R. glandulosum, R. hirtellum,* and *R. lacustre.* Leaves of various ages were present on all the plants. The mature ones showed infection first. The degree of infection was heaviest on the first species and decreased in the order named, *R. lacustre* having but two pustules on a single leaf. Later, the half-mature leaves of *R. nigrum* and the leaves of *R. triste* and *R. glandulosum* two-thirds mature became infected. The younger leaves did not become infected then, but when reinoculated later they took the disease, except that those of *R. lacustre* remained healthy. In most inoculation tests made by the writer and his associates in the greenhouse both the oldest and the youngest leaves remained free from disease, although they were treated exactly like the others. York[27] tested this point extensively in the open in 1918 and found that leaves just unfolding were almost invariably immune to the fungus; older ones took the disease readily; and overmature ones (especially late in the season) were immune. Pennington[28] reached similar conclusions working independently.

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[27] York, H. H. Op. cit.

[28] Pennington, L. H. Op. cit.

Snell [29] made inoculations out of doors with spores from unopened æcia on April 30, 1918. He inoculated opening buds of *Ribes glandulosum* by carefully inserting a knife so as not to injure the leaflets and inserting the spores between the folds of the leaves. The largest leaves were 3 cm. broad, the smallest 3 to 5 mm. long. It was very rainy, so there was plenty of moisture. No infection was visible on May 15, but on May 22 heavy infection was present on all the leaves inoculated. The leaves on this date ranged from nearly full size to those just opening. The infection was heaviest on the largest leaves inoculated and decreased to a light infection on the smallest. The check plants were healthy. There are two possible factors which might have delayed the infection a week longer than usual. These are cool temperature and the immaturity of the leaves. The experience of the writer leads to the belief that the latter was the principal factor involved in this case. Later Snell found natural infection on leaves of *Ribes vulgare* that were only 12 mm. wide.

It has been noted repeatedly that the earliest infections on Ribes leaves in the spring are about a month later than the time when the first æciospores are set free. It is a question whether this is due to very cool nights or to the immaturity of the Ribes leaves at this time. Noninfection of immature leaves in the greenhouse leads the writer to suspect that the latter is the main factor involved. European writers (63, 101) have stated that *Cronartium ribicola* is decidedly earlier than the native pine-stem Peridermiums.

Observations made by Gravatt at Block Island show that new infection in midsummer was present upon the fifth to the eighth leaves from the tip, not counting those less than 5 mm. wide; that is, on leaves just mature but not hardened.

Gravatt and York and Overholts made many inoculations of leaves, petioles, and stems with wounds, but found no evidence that infection was favored by wounds.

Whether viability of spores of *Cronartium ribicola* in culture solutions, water, etc., is a reliable index of their infective power (43) is a question which has arisen more or less insistently since inoculation experiments began. Klebahn (70) made a definite test with reference to this question with æciospores of *Cronartium ribicola*. The spores were collected on March 20 and kept dry until May 8 when the test was made. Some were sown on the leaves of *Ribes aureum*, some were sown on a cover glass coated with a thin layer of sterile Ribes-decoction agar, and others were sown on a cover glass moistened with water. The cover glasses were kept in a moist chamber to prevent drying. The Ribes plants became infected after 12 days on every leaf inoculated. The spores on Ribes-decoction agar germinated

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[29] Snell, W. H. Period of exposure and size of Ribes leaves infected by the blister-rust fungus. Seen in manuscript. To be published in Phytopathology.

slowly at first, but later developed strong germ tubes in considerable quantity. Scarcely a spore in water germinated. As a result of his extensive experience with the rusts, Klebahn says:

> . . . in other words, I believe it possible for spores which do not germinate in water to infect leaves of the host plant, and it seems to me to be expedient to distinguish between "infection power" and "viability" of spores more sharply than is ordinarily done.

Gravatt had experiences somewhat similar to the above in his inoculations with urediniospores of *Cronartium ribicola* in 1917. So pronounced has been our general experience in this regard, that many germination and longevity culture tests made in 1918 and 1919 were duplicated by check inoculations on favorable hosts so far as possible.

LOCATION OF THE INFECTIONS ON RIBES PLANTS.

SORI ON THE LEAVES.

The usual place for uredinia and telia of *Cronartium ribicola* to form is on the lower side of the Ribes leaf blade. It is rather exceptional for them to appear elsewhere. Nevertheless, they are occasionally found on the upper side of the leaf blade. They have been noted there by Gravatt in the greenhouse and by several out-of-door workers on Block Island. The following species have been seen with uredinia or telia on the upper leaf surface: *Ribes alpestre*, *R. aureum*, *R. cereum*, *R. fasciculatum*, *R. fontenayense*, *R. hirtellum*, *R. odoratum*, and also the horticultural varieties *R. aureum* var. Utah Yellow and *R. vulgare* var. White Imperial. It must not be concluded that because fruiting bodies are found on the upper surface of leaves that the infection took place there. On the contrary, in every case seen, it was very evident that the fungus had attacked the infected leaf beneath, and the attack had been so intensive that some sori were pushed through to the upper surface. There never were as many sori on the upper surface as there were on the lower one, nor were they so old.

Some inoculations have been made in Europe to determine if infection may take place on the upper surface of Ribes leaves. So far as known to the writer they are here summarized:

In 1913 Ewert (37) brought four potted plants of *Ribes nigrum* into the greenhouse. On April 10 he inoculated the leaves of one branch of plant 1 on the lower surface only with fresh æciospores. The plant was inclosed in a glass cylinder as a moist chamber. Another branch was used as a check. On April 28 the inoculated branch bore uredinia upon 11 leaves. On April 15 he inoculated the leaves of a third branch, but did not inclose it in a moist chamber. On April 26 there was no sign of infection, and it was then inclosed in a moist chamber. On May 20 all the inoculated leaves bore uredinia. The control remained healthy.

Plant 2 was treated exactly like plant 1 except that the inoculations were made on the upper sides of the leaves. No infection resulted.

Plant 3, on April 10 and 15, was inoculated on one branch on only the lower surfaces of the leaves. Another branch was inoculated on the upper surfaces only. A third branch was left as a check. Weak infection resulted on the first branch. A repetition on April 29 with fresh æciospores gave better results.

Plant 4, left untreated, was in another inclosure of the greenhouse. It remained healthy, showing that infection had not occurred before the plants were brought into the house.

On May 26 similar inoculations were made by Ewert with urediniospores on the upper sides and lower sides of leaves. Infection resulted in the latter case and also a slight infection of the lower surface of one leaf which was inoculated on the upper surface.

Another similar series of inoculations made by Ewert on June 6 gave infection only on the leaves inoculated on the lower side. He fails to say in all cases that the sori formed only on the lower surface of the leaves, but his language implies that this is the case. Attacking the problem in another way, Ewert (37) sprayed *Ribes nigrum, R. aureum,* and *R. rubrum,* leaves, part on the lower side only, part on the upper side only, and part on both sides, while controls were left unsprayed. The details are presented on pages 77 to 79. Because some leaves which were sprayed on the upper side developed a few sori beneath, he appears to be a little doubtful whether infection may occur on the upper surface, but he concludes that it "apparently almost exclusively takes place on the lower surface of the leaf."

The writer and his associates have made hundreds of inoculations on the upper surface of leaves of many species and varieties of Ribes, without a single direct infection occurring there. Numerous instances have been noted in these experiments in which infection appeared on the lower surfaces of leaves that had been inoculated on the upper side. This is believed to be due to spores reaching the lower surface in some unknown way. In fact it is very difficult if not impossible to guard against this. York and Overholts inoculated leaves of *Ribes glandulosum* on the upper side, both with and without ring cells, to prevent the spores reaching the lower surface. Slight infection occurred on the lower side in some cases where cells were not used. Where the cells were used no infection occurred. These tests were made on leaves of different ages on plants of various ages, from young seedlings up to fruiting bushes. Tubeuf (173) inoculated leaves of *Ribes nigrum* on the upper side by applying the spores in water with a brush. All of the leaves thus inoculated remained healthy except a single one which had a uredinium on the lower surface. He was uncertain whether a spore infected it through the lower surface or through a lesion on the upper surface.

SORI ON COTYLEDONS.

The cotyledons of young Ribes seedlings are apparently quite susceptible to infection by æciospores and urediniospores of *Cronartium ribicola*. Relatively heavy infection has resulted from inoculations on the lower surface of cotyledons of *Ribes americanum, R. missouriense, R. oxyacanthoides, R. rotundifolium, R. glandulosum*, and *R. fasciculatum* seedlings in the greenhouse and on *R. glandulosum* in the field.

SORI ON FLORAL BRACTS AND BUD SCALES.

Infection was secured by Gravatt from inoculations of the floral bracts of *Ribes aureum* in several different cases in the greenhouse.

Infection of opening buds and of bud scales merits more investigation. McCubbin (85) suggested the possibility of infection of partially open buds in the fall and the overwintering of the fungus, but he could not prove that it occurs. Infection of young leaves scarcely out of the bud occurs, but it seems to be limited to leaves that are relatively mature, though small. (See discussion on pp. 44 to 46.) Search for infections of buds on heavily infected *Ribes nigrum* bushes failed to reveal any infections (151, p. 44). Gravatt made inoculations of buds about to open, but with no success. York[30] has inoculated successfully an inner bud scale of *Ribes nigrum*.

SORI ON PETIOLES.

Next in frequency to infection of the lower surface of the leaf blade is infection of petioles. The first published account of this, so far as the writer knows, was given in 1912 (133, 134, 135) and 1913. At that time it was considered to be very uncommon. Since than a considerable number of such cases have been noted both in the greenhouse and out of doors. The following species have developed uredinia or telia, or both, upon petioles, as many as 25 or more petioles on a single plant being thus attacked: *Ribes americanum, R. aureum, R. bracteosum, R. cereum, R. culverwellii, R. cynosbati, R. divaricatum, R. erythrocarpum, R. fasciculatum, R. giraldii, R. glandulosum, R. inerme, R. lacustre, R. nevadense, R. nigrum, R. parishii, R. petraeum, R. robustum, R. setosum*. The following cultivated varieties have had petiolar attacks: *Ribes nigrum* hort. vars. Black Victoria, Climax, and Seabrook Black; *R. reclinatum* hort. vars. Berkeley, Golden Prolific, Poorman, Transparent, and Van Fleet; *R. vulgare* hort. var. White Imperial. Some 10 or 12 as yet unidentified species collected by Beattie in the Rocky Mountain and Pacific coast regions have exhibited the same phenomenon.

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[30] York, H. H. Op. cit.

In many cases the petiole became diseased by growth of the mycelium downward from the leaf blade into it, but direct infection of the petiole occurs occasionally. This is shown by the presence of infections on the petiole one-half inch or more distant from other infections. Microscopic examination by Colley in such instances has shown the intervening tissues to be entirely free from migrating mycelium. York [31] had several instances where infection took place well down on the petiole, and no other infection was present either on that petiole or the leaf blade. While many inoculations of petioles have been made by members of the Office of Investigations in Forest Pathology, but few have been successful, as above indicated.

SORI ON STEMS.

Evidence of infection of Ribes stems has long been sought. In 1917, Posey, Gravatt, and Colley (112) discovered three uredinia on young stems of *Ribes hirtellum* which resulted from natural infection in an outbreak area. Artificial inoculations on young stems of the same species with æciospores produced 18 more uredinia. A single stem infection was produced by Gravatt in the greenhouse upon a young seedling of *R. fasciculatum* (Pl. V, fig. 2). Æciospores were used in this case also. While the tender stem was completely girdled, it survived long enough to form wood and finally completely outgrew the disease. Since then Taylor has successfully inoculated with æciospores the stems of young seedlings of *Ribes missouriense* and of *R. americanum* in the greenhouse. York has infected stems of young *R. glandulosum* plants with æciospores and uredinicspores out of doors, and has found natural infections on the same species and on *R. cynosbati*. He has infected a young stem of a 2-year-old plant of *R. cynosbati* with æciospores in the greenhouse.

RELATION OF STOMATA TO THE INFECTION OF RIBES.

A number of investigators of the Uredinales have stated that æciospore and urediniospore germ tubes obtain entrance to their hosts through the stomata (34, 70, 110, 149, 171).

As heretofore stated, *Cronartium ribicola* infects the Ribes plant on the lower side of the leaf mostly. Less frequently it infects the petioles, floral bracts, and cotyledons. It may infect young stems. Infection never occurs on the upper surface of the leaf. Examination of a number of different species of Ribes has been made by members of the Office of Investigations in Forest Pathology. Data on the stomata may be summed up as follows:

> Stomata were present in large numbers on the lower surface of leaves of all species examined. Stomata were present in small numbers on the upper surface of leaves of *Ribes cereum* (60, 78), *R. inebrians* (60, 78), *R. odoratum* by Marshall, *R. orientale* (160), and

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[31] York, H. H. Op. cit.

A. Hoen & Co Baltimore

LEAVES AND PLANT OF RIBES, SHOWING INFECTIONS OF CRONARTIUM RIBICOLA.

FIG. 1.—Upper surface of a leaf of *Ribes cynosbati* infected by *Cronartium ribicola*. Early stage of dying of the leaf tissue. FIG. 2.—Seedling plant of *Ribes fasciculatum* with stem infected by *Cronartium ribicola* as a result of inoculation with æciospores. FIG. 3.—Upper surface of an infected leaf of *Ribes reclinátum*, horticultural variety Smith. This is quite resistant. Leaf tissue already dead. FIG. 4.—Upper surface of infected leaf of *Ribes vulgare*, horticultural variety Palluau. Quite resistant. A more advanced stage in death of attacked leaf tissue. Painted by J. M. Shull.

R. vulgare by Marshall. None were found by Unger (176) on the upper surface of leaves of *R. alpinum* nor by Taylor on *R. americanum, R. aureum, R. carrierii, R. culverwellii, R. fasciculatum, R. nigrum, R. reclinatum, R. speciosum, and R. (tenuiflorum) aureum.* Stomata were found only on the lower surface of cotyledons of *R. fasciculatum* and *R. missouriense*, the only ones examined by Taylor. Stomata were found by Taylor to be not uncommon on petioles of *R. americanum, R. aureum, R. carrierii, R. culverwellii, R. hirtellum, R. inerme, R. nigrum, R. odoratum, R. reclinatum, R. sanguineum, R. speciosum, R. succirubrum, R. (tenuiflorum) aureum*, and *R. vulgare.* None were found on petioles of *R. curvatum* and *R. fasciculatum.* Janczewski (60) states that stomata are present on the young stems of *R. petraeum.* A few stomata were found on young stems of *R. aureum, R. hirtellum, R. nigrum, R. odoratum, R. reclinatum, R. succirubrum, R. (tenuiflorum) aureum*, and *R. vulgare.* None were found on the stems of *R. carrierii* and *R. fasciculatum.* These findings compare well with the inoculation results, if stomata are the avenue for infection. It is perhaps to be expected that infection may be produced on the upper surface of the leaves, but only very rarely. Colley (20) found young uredinia forming in the substomatal spaces, which would indicate that infection took place in that vicinity and presumably through the stomata. York [32] found germ tubes of æciospores entering the stomata of leaves of *Ribes cynosbati, R. glandulosum*, and *R. nigrum.*

VARIATIONS IN APPEARANCE ON RIBES LEAVES.

The study of great numbers of Ribes leaves infected in the greenhouse and of very numerous specimens of diseased leaves collected in the field from Maine to Minnesota, during the past ten years, has revealed some distinct variations in the appearance of the fungus and of the diseased leaves of different species and varieties of Ribes. Previous study of such differences seem to have been made chiefly by Hennings (52, 53).

BLISTERY APPEARANCE OF THE UREDINIA.

In August, 1916, there occurred a very hot, dry period in New England. This was followed by the finding of a few very peculiar-looking uredinia on *Ribes nigrum* and *R. vulgare.* Under a hand lens, the uredinia were not of the usual mealy appearance, but looked more like tiny blisters. Examination showed that the epidermis of the leaves had become toughened, so that the uredinia did not burst through it, as they usually do, but pulled it loose from the inner leaf tissues and in this way actually formed small blisters. The urediniospores never broke through it. From the weather conditions preceding and at the time this occurred it is believed that the dry, hot weather rendered the epidermis tougher than usual. It is a rare occurrence, as only a few cases have been noted. In 1916, one specimen came from each of the States of Massachusetts, Maine, and Vermont. In 1917, a single case was found in New Hampshire. Hedgcock noted this in 1919 upon artificially inoculated Ribes bushes on Block Island. Recently, blisters have been noted on *R. auruem* and *R. fasciculatum* in the greenhouse.

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[32] York, H. H. Op. cit.

DISTRIBUTION AND SIZE OF THE SORI AND COLONIES.

It has been found that *Cronartium ribicola* forms its uredinia and telia upon each species of Ribes in a manner which in general is characteristic of that host species (Pls. IV; V, figs. 1, 3, and 4; and VI). This was noted in 1902 by Hennings (52, 53), who described some of the more striking variations. Like all general statements, the following are subject to individual variations from the normal or average condition for the host species. A statement by Hennings (52, p. 130) indicates the degree of variation discernible to a keen observer:

> It is especially noticeable that the fungus, according to the character of the leaves of various species of Ribes, shows great variations in the form and color of the spots produced on the leaves, the form and size of the sori, and the size of the telial columellæ, so that a new observer would assume that several of the fungus forms were specifically distinct.

In general, on species which are closely related, or which closely resemble each other, the fungus behaves in a similar manner. Some of the more striking variations are described as follows:

RIBESIA.[33]—*Ribes petraeum* and var. *atropurpureum:* Sori close together and evenly distributed over the spots; spots large, soon overrunning a large part of the leaf surface.

Ribes rubrum vars. *petrowalskyanum*, *pubescens*, and *sibirica:* Very scant sori, located beside large veins of leaf; var. *scandicum* has abundant sori, close together, generally distributed.

Ribes triste: Sori clustered on definite spots; spots small, widely separated.

Ribes vulgare: Sori not plentiful, clustered on spots; spots small and isolated (Pl. IV, fig. 3; V. fig. 4).

HERITIERA.—*Ribes coloradense:* Sori thickly clustered on diffuse spots.

Ribes glandulosum: Sori usually thinly scattered over large diffuse spots or entire leaf surface, telia very slender and long (Pl. VI, fig. 1).

Ribes erythrocarpum: Sori plentiful, clustered.

CALOBOTRYA.—*Ribes glutinosum:* Sori thickly clustered in local areas.

Ribes nevadense: Sori thickly grouped on local spots; spots large and distinct.

Ribes viscosissimum: Sori isolated, scattered over entire leaf surface.

SYMPHOCALYX.—*Ribes aureum* and vars. *tenuiflorum* and *palmatum:* Sori abundant, closely grouped in rather distinct spots which usually are well separated from each other (Pl. IV, fig. 1).

Ribes odoratum: Sori abundant, closely grouped in spots usually well separated from each other.

AROPHYLLUM.—*Ribes cereum:* Sori clustered on definite rounded spots which soon die.

Ribes inebrians: Sori on rounded spots.

EUCOREOSMA.—*Ribes americanum:* Sori sparse and scattered, on small irregular spots which redden and die; heavy infection rare; telia short, one-half to 1 mm.

Ribes bracteosum: Sori plentiful, on large diffused spots or patches of leaf surface.

Ribes nigrum (Pl. IV, fig. 4) and vars. *aconitifolium*, *fasciculatum*, "*folio argentea*": Sori crowded densely, often over entire leaf surface, vigorous; telia abundant, reaching 2 mm. in length.

Ribes viburnifolium: Sori scant, dead spots form early.

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[33] The species of Ribes are grouped according to the arrangement of Janczewski (60).

GROSSULARIOIDES.—*Ribes lacustre:* Dead spots formed early on infected leaves; sori sparse or diffuse, irregular spots; telia rather scattered.

GROSSULARIA.—*Ribes lobbii:* Sori thickly crowded on rounded spots, telia well developed.

Ribes menziesii: Sori sparse on small irregular spots.

Ribes speciosum: Sori seated closely together on large rounded spots, telia rather short.

EUGROSSULARIA.—*Ribes alpestre:* Sori thickly crowded on large rounded spots, telia short.

Ribes curvatum: Sori crowded on rounded spots on young leaves, on irregular spots on old leaves; telia quite plentiful; spots with reddened edges late in season.

Ribes cynosbati: Sori plentiful on definite spots, which are usually rounded (Pl. V, fig. 1); spots sometimes wedge shaped, lying between two branching veins of the leaf; telia crowded in small groups, 1 to 1½ mm. long, rarely over entire leaf surface.

Ribes divaricatum: Sori scattered on rounded spots.

Ribes missouriense: Sori crowded on rounded indefinite spots on young leaves, densely crowded on small leaves, dead irregular spots on old leaves.

Ribes leptanthum: Sori very scant; dead spots appear so early that uredinia can form with difficulty, often only one uredinium on a spot, many spots without sori; produces the least sori of any species yet noted.

Ribes hirtellum: Sori usually crowded thickly on small spots; uredinia on small rounded spots; telia small, crowded densely; on older leaves, on small indefinite, irregular spots bounded by veinlets; spots sometimes purplish on the edges.

Ribes oxyacanthoides: Like *R. hirtellum.*

Ribes reclinatum: Sori rather sparse, on small irregular spots of dead tissue. There is a tendency toward a reddening or purpling of the edges of the spots on old leaves. (Pl. V, fig. 3.)

Ribes rotundifolium: Sori crowded on small irregular spots. The spots die early and are likely to become reddish around the edges even on rather young leaves. It is rather rare for the entire leaf to become covered with sori.

Ribes setosum: Much like *R. cynosbati.*

HEMIBOTRYA.—*Ribes fasciculatum* vars. *chinense* and *japonicum:* Sori densely crowded on large rounded spots.

DIACANTHA.—*Ribes diacantha:* Sori on rounded spots.

Ribes giraldii: Sori scattered on rounded spots.

In general, it may be said that *R. nigrum* and its varieties is the optimum host species among the Ribes for *Cronartium ribicola. Ribes aureum* and *R. odoratum* and their varieties are perhaps next to *R. nigrum* in favoring the growth of the fungus. *R. reclinatum* does not take the disease readily, but is by no means immune to it. In fact, no species or variety yet fully tested is entirely immune. *R. leptanthum* probably produces fewer sori for the extent of infection than any other species. This is caused by the very early death of the infected tissue.

PALE COLOR OF INFECTED SPOTS ON THE LOWER SURFACE OF RIBES LEAVES.

The production of sori on an infected spot on the lower surface of Ribes leaves is often preceded for one, two, or three days by a pale coloration (Pl. VI, fig. 2). This is most likely to occur on young leaves. It is a fairly certain symptom of a successful inoculation.

Striking cases of the preservation of the normal green color in the infected areas, while the rest of the leaf is etiolated, have been noted a number of times.

PALE COLOR OF INFECTED SPOTS ON THE UPPER SURFACE OF RIBES LEAVES.

Numerous young Ribes leaves inoculated in the greenhouse developed pale spots on the upper side of the infected leaves (Pl. V, fig. 1). These varied from nearly white to yellow. Similar spots are often seen in the field. Some species of Ribes seem to be more likely to develop these spots than others. Among those showing this etiolation as a result of infection by *Cronartium ribicola* may be mentioned: *Ribes aureum* and its varieties, *R. cereum*, *R. cynosbati*, *R. divaricatum*, *R. erythrocarpum*, *R. fasciculatum*, *R. glandulosum*, *R. hirtellum*, *R. inebrians*, *R. inerme*, *R. leptanthum*, *R. nevadense*, *R. nigrum*, *R. odoratum*, *R. reclinatum*, *R. rotundifolium*, *R. setosum*, *R. speciosum*, *R. triste*, and *R. vulgare*. These spots seem to be produced by conditions existing in the immature Ribes leaf when attacked by the fungus very actively.

REDDENING OF INFECTED SPOTS ON RIBES LEAVES.

Certain species of Ribes react to infection by *Cronartium ribicola* by a reddish or purplish coloration around the edges of the infection. This is common with some species, while others apparently must have the leaves at a certain stage of maturity for this coloration to occur. *Ribes americanum*, *R. curvatum*, *R. rotundifolium*, *R. viburnifolium*, *R. glandulosum* (old thick leaves), *R. cynosbati* (old thick leaves), *R. hirtellum* (old thick leaves), *R. oxyacanthoides*, *R. reclinatum*, and *R. missouriense* develop the red color in the order named.

DEAD AREAS OF INFECTED LEAF TISSUE.

Where the attack of *Cronartium ribicola* is intense, areas of the oldest infected tissue of the diseased leaves collapse and die (Pl. V, figs. 3 and 4; Pl. VI, fig. 3). The different species of Ribes vary much in this respect, some developing dead spots very quickly and some doing so only after considerable time. *Ribes nigrum* usually resists death tenaciously. When a spot dies it is commonly a large one and soon results in the premature fall of the affected leaf. At the other extreme is *R. leptanthum*. With this species the infected spots die very quickly, even before uredinia can form (147). Less than 10 per cent of these spots produce any uredinia or telia, and those few spots bearing sori usually have only from one to several stunted sori. All species of Ribes tested have sooner or later developed dead spots. Just how much secondary fungi contribute to the killing of host tissues is entirely unknown.

LEAVES OF RIBES INFECTED WITH CRONARTIUM RIBICOLA, SHOWING DIFFERENT TYPES OF INFECTION.

FIG. 1.—Infected leaves of *Ribes glandulosum*, showing lower surfaces; the sparsely scattered telia are well distributed over the entire surface. Etiolation caused by the disease is also evident. $\times \frac{5}{8}$. FIG. 2.—Lower surfaces of leaves of *Ribes* sp., showing etiolated spots where infection has taken place, two days before uredinia were formed. $\times \frac{5}{8}$. FIG. 3.—Lower surfaces of infected leaves of *Ribes aureum*, showing the disease distributed in local spots mostly well separated from one another. On the right side of the right leaf a large area of leaf tissue has died. Etiolation from the disease is evident. $\times \frac{5}{8}$.

THE UREDINIA AND UREDINIOSPORES.

GENERATIONS OF UREDINIA.

In 1918, Pennington[34] and Snell investigated the number of generations of uredinia of *Cronartium ribicola* produced in the Adirondack region, and the weather conditions that might influence their production. *Ribes rotundifolium, R. cynosbati,* and *R. glandulosum* were the principal species used in these investigations. The observations were made in four different localities within 10 miles of the town of Lewis. There were seven periods of uredinial production in 1918. The first generation began on May 28, reached its climax about June 12, and then gradually fell off until June 26 to 28, when the second appeared. The third began to appear about July 12 and reached its maximum on July 19 to 22. The second and third crops of uredinia were located almost entirely on those leaves which were originally infected by æciospores or those adjacent to them. Drought from July 18 to July 28 caused most of the infected leaves to drop from the bushes of *Ribes cynosbati* and *R. rotundifolium,* leaving them partly or entirely defoliated. The fourth crop was much smaller, but well marked, and came on August 19 and 20. The fifth generation came on September 12 to 15; it would have been more abundant had not a heavy frost on September 11 killed all the leaves of *R. glandulosum* and some on the other two species of Ribes. The sixth crop appeared especially on the second crop of leaves of the earlier defoliated bushes and on fresh green leaves of bushes in sheltered situations. The seventh generation appeared on October 15 to 18 on leaves ready to fall. A study of the weather conditions, as noted at Lewis, showed that about two weeks before the appearance of each new generation there was a period of at least 24 hours of rainy and cloudy weather. But not all such periods were followed by new crops of urediniospores.

In 1919, Pennington[34] found that the generations of uredinia were not as distinct at Lewis, N. Y., as they were in 1918. The first four, on May 23, June 21 and 22, July 3, and July 20, respectively, were well defined. A fifth on August 7 and a sixth on August 21 were distinct on some bushes, but in most places overlapped. In general, after August 1, the generations overlapped, because of rain every day or two, so as to become confused with each other.

SEASON OF PRODUCTION OF THE UREDINIA.

Like the æcial season, the beginning of the uredinial season of production varies with conditions somewhat, though to a less marked degree. May 16 is the earliest recorded date for mature uredinia. A week after this is the more usual time for them to be found in most

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[34] Pennington, L. H. Op. cit.

localities. (For range of observed dates in various sections of North America, see Table V, p. 72.)

In the White Mountain region of New Hampshire, York[35] found fresh urediniospores in 1918 on May 16 and as late as November 17. Urediniospore production there continued on some bushes for 185 days, while under average conditions it continued about 120 days. At this place the following species were under observation: *Ribes cynosbati, R. glandulosum, R. lacustre, R. nigrum, R. odoratum, R. oxyacanthoides, R. reclinatum, R. triste,* and *R. vulgare.* Urediniospore production continued the longest time (185 days) on *R. nigrum* and the shortest time (65 days) on *R. lacustre.* In general, it can be stated that the urediniospores continue to form as long as there are susceptible leaves on the Ribes bushes of a given locality.

York[35] found that the maximum urediniospore production in 1918 occurred about July 14 to 16 and in 1919 about July 25 to 26. After these dates came the maximum sporidia production, and then the bushes became almost completely defoliated.

DISTANCE OF DISSEMINATION OF THE UREDINIOSPORES.

In the early work upon *Cronartium ribicola* in North America the wide dissemination of the fungus from a given center appeared to take place by means of the urediniospores. Stewart and Rankin (151), who had an especially good opportunity to study this point, concluded that the urediniospores were blown at least one-half mile. Early general observations of the spread of this stage indicated that a wet season greatly favored it, while a dry season just as markedly retarded it.

McCubbin (87) found that urediniospores fall in still air about 8 feet in 5 minutes. He calculated that a 30-mile breeze would carry them 2½ miles in this time. Theoretically they may be distributed long distances if located on a hill or if picked up by convection air currents. But most of these spores are actually produced within 2 feet of the ground in most localities, so that they are not picked up by the wind as readily as the æciospores, which are commonly produced a number of feet above the ground. When set free, the urediniospores adhere in masses, so that they are not as readily blown by the wind as are the æciospores, which tend to fall apart when dislodged from the æcium.

York and Overholts (cited in Spaulding, 145) in 1918 at North Conway, N. H., found urediniospores in spore traps up to 300 yards distant from the known source. This was where rain was plentiful practically all summer. Observations on infections of *Ribes glandulosum* and *R. cynosbati* plants indicated that the disease spread by urediniospores up to 100 yards. In some cases where the bushes

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[35] York, H. H. Op. cit.

were protected by surrounding trees or other objects, the rust spread little or not at all. In other words, where moisture was plentiful through the season, the distance of spread by urediniospores was governed by factors controlling the free access of the wind. In Essex County, N. Y., drought prevailed through July and August in 1918. Here Pennington[36] worked with spore traps and Snell (128) gave special attention to a study of the spread of the uredinial stage on Ribes. The Ribes of this section were largely *Ribes rotundifolium* and *R. glandulosum*. Here the rust spread in most instances only to adjacent leaves from those first infected on a given bush. The spore traps here caught urediniospores only at a very short distance, 50 feet or less.

In 1919, York (cited in Spaulding, 146) caught urediniospores up to a distance of 3,400 feet in an open location, but they did not germinate. Urediniospores caught at 3,200 feet did germinate. Pennington[36] caught urediniospores up to 156 feet.

AGENTS DISSEMINATING THE UREDINIOSPORES.

Wind has been supposed to be the principal agent distributing the urediniospores of *Cronartium ribicola*. While this supposition is correct in the main, other agents are concerned in the matter.

Hennings (53) says that sprinkling diseased Ribes plants with a strong stream of water carries urediniospores from plant to plant. Rain accompanied by high wind is known to carry spores of some plant diseases (38, 44). It is entirely possible for this to occur with any spore capable of wind distribution, as in the present case.

In 1917 Gravatt and Marshall (45) made studies in the experimental greenhouse at Washington, D. C. They found that weevils, snails, slugs, and sow bugs fed on the uredinia and telia of *Cronartium ribicola* on the diseased plants. The ingested urediniospores lost their viability to a large extent, but not entirely.

In the same year Gravatt and Posey (46), working at Kittery Point, Me., found that gipsy-moth larvæ feed quite freely upon leaves of *Ribes hirtellum* and *R. vulgare* and that in some cases the only infected leaves were those which had been partially eaten by insects, indicating that they carried the spores which infected the leaves. The insects were found carrying viable urediniospores on their bodies. There can be no doubt that these insects play an important rôle in the local distribution of this fungus within the gipsy-moth infested area.

Studies by Snell (127) at Lewis, N. Y., in 1918, show that a large number of insects visit Ribes plants during the season when the rust is present upon the leaves. The spore-laden insects were inclosed in chambers with the tips of *Ribes glandulosum* plants, and infection

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[36] Pennington, L. H. Op. cit.

resulted in due time. Many of these insects are, of course, accidental visitors, but quite a number feed or breed upon the Ribes plants. All of those which frequent the Ribes bushes by preference may carry many spores of both uredinia and telia. Such insects would be most likely to spread the disease, since upon leaving one Ribes plant they would seek another, thus scattering the spores exactly where they could start new colonies of the disease. But the accidental visitors, in a locality where Ribes bushes are abundant, could also spread the spores locally, but in a much more indiscriminate manner, so that but a very small percentage of the spores would ever reach leaves of Ribes.

Aside from carrying spores on their bodies, some insects feed directly on the uredinia and telia and a few of the excreted spores are known to retain their viability. Still other insects may be leaf eaters and ingest the rust spores only accidentally. These would be of minor importance in spreading the disease.

At Lewis, N. Y., where the Ribes bushes overhang narrow cattle paths which wind through a heavy cover of blackberry, raspberry, and other low shrubs, observations by Pennington and Snell indicate that cattle, sheep, horses, dogs, and berry pickers may carry the urediniospores from an infected bush to neighboring healthy ones.

The remarks on the carrying of æciospores by automobiles, steam trains, and electric cars on page 36 apply also to some extent to the urediniospores.

GERMINATION OF THE UREDINIOSPORES.

The urediniospores of *Cronartium ribicola* have been generally found to be erratic in germinating. At one time excellent germination occurs; at another, none at all. In the greenhouse experiments it seems that urediniospores produced in newly formed uredinia have greater infective power than those produced later in the same uredinia. Such early urediniospores seem to give as good results as fresh æciospores. The former are usually produced in limited quantities while the latter are usually abundant. This results in a more liberal use of the latter, so that a fair comparison of the two is not possible from the usual inoculation work. Gravatt made comparative tests and concluded that æciospores and urediniospores from newly open sori were about equal in infective power. More such tests should be made before any conclusive statement is made on this point.

Gravatt and York found that newly matured urediniospores produced out of doors were decidedly more viable than older ones. This agrees with general experience in making inoculations in the greenhouse.

Gravatt found that cooling the urediniospores on ice stimulated germination. Uncooled spores gave 15 to 23 per cent germination while ice-cooled ones of the same lot gave 25 to 54 per cent germination. Marshall found the same stimulating effect from a temperature of 23° F. upon urediniospores on Ribes leaves stored outside a window, as compared with those on leaves kept at room temperature.

Posey dried infected leaves of *Ribes nigrum* in the hot July sun for four hours. Urediniospores from these gave germination ranging from 3 to 45 per cent, with an average of 17 per cent. Spores from other leaves collected at the same time and dried inside in the shade gave 3 to 90 per cent germination, an average of 47 per cent. During dry, hot weather it has been found that the viability of the urediniospores out of doors is very low.

Duff (30), in studying the factors affecting their viability, found that exposure to bright sunlight reduces their germination, the ultraviolet rays being the destructive agent. Their viability appears to him to be low. Three days after collection less than 50 per cent germinated in distilled water. In about two weeks germination was negligible even when stimulated by cooling to 2° to 5° C.

Pennington [37] made germination tests of newly-matured urediniospores of *Cronartium ribicola* produced naturally in the vicinity of Lewis, N. Y., from early June until late in the autumn in hanging drops of tap water. During the first two weeks of June (frequent rain) the percentage of germination was high. From June 16 to 28 no tests were made. On June 29 and July 1 (rather dry) only 1 per cent germinated. After this time, many tests were made with spores from various localities. By July 14 (very hot alternating with some rain) less than one-third of 1 per cent germinated, and from July 22 to 26 (hot and dry) less than one-tenth of 1 per cent. Fresh yellow spores kept in an ice box gave no better results. On August 1 (rain July 29 and 30) 5 per cent germinated. After this (decidedly more rain) from 10 to 40 per cent germinated. The viability of these spores seemed to be greatly decreased by hot, dry weather and increased by cool rainy spells at the time they were produced. When the number of spores produced decreased because of hot, dry weather, their rate of germination also decreased and vice versa.

Doran (28) found that the limiting temperatures for the germination of urediniospores are: Minimum 8°, optimum 14°, and maximum 25° C. He calls attention to the fact that—

> There is apparently a relation between the season when spores occur and their temperatures for germination. The æciospores of *Cronartium ribicola* occur in the spring when the average temperature is lower than in the summer, the season of occurrence of the urediniospores of this fungus. The æciospores of this fungus have a minimum temperature for germination, which is 3° C. lower than that of the urediniospores; an optimum 2° C. lower than that of the urediniospores; and a maximum 6° C. lower than that of the urediniospores.

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[37] Pennington, L. H. Op. cit.

Germination of fresh urediniospores usually takes place readily in tap water. Gravatt found that distilled water gave poorer germination than tap water. Colley (20) found that the germ tube pushes through the exospore without the aid of a germ pore. The contents of the spore soon pass into the young germ tube, which may extend some distance over the surface of a Ribes leaf. Entry to the interior of the leaf appears to be through the stomata. The urediniospores germinate in about five and one-half hours (28) in drops of distilled water on glass slides.

During germination studies in 1918, York[38] occasionally found germinating urediniospores which formed secondary conidia. An investigation of the conditions causing their formation showed that newly formed urediniospores usually do not produce the secondary conidia in tap water, while old urediniospores were more likely to produce them. The following species produced them, the frequency increasing in the order named: *Ribes lacustre*, *R. cynosbati*, *R. vulgare*, *R. reclinatum*, and *R. nigrum*. Urediniospores from *R. glandulosum* did not produce secondary conidia. Urediniospores exposed in bags of mosquito netting out of doors gave especially abundant secondary conidia. Urediniospores from *R. nigrum* produced secondary conidia in weak solutions of ammonia, maltose, tannic acid, gallic acid, malt extract plus gallic acid, lactose plus tannic acid, and lactose plus gallic acid. They were especially abundant in the last solution. They were not produced in pine decoction, weak solutions of ether, lactose, maltose plus tannic acid, and maltose plus gallic acid. A limited number were produced in water. They form on the ends of the germ tubes or laterally and are capable of producing a germ tube themselves. Similar secondary conidia have been noted by Tulasne (175) in cultures of *Cronartium asclepiadeum*, and they have been noted by Plowright (109) and Sappin-Trouffy (122) in other Uredinales.

LONGEVITY OF THE UREDINIOSPORES.

The first experiments in testing the longevity of urediniospores of *Cronartium ribicola* seem to have been carried out by McCubbin[39] in 1916. His manuscript account of these experiments follows:

> The spores used for this series were all collected on the same day. They were dried on paper for a few hours and then placed in a number of small bottles plugged lightly with cotton, the contents of each bottle being available for a single inoculation. Half of these bottles were kept on a shelf in the laboratory, where they were dry and exposed to weak light, and the other half were placed under a bell jar on the soil in a garden, exposed to changes of humidity, temperature, and light.
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> At stated intervals a bottle was taken from each set and the spores within were shaken up with a small amount of distilled water. By the use of a small atomizer the suspension of spores was then sprayed on the under side of the leaves of small

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[38] York, H. H. Op. cit.

[39] McCubbin has very kindly allowed the use of his unpublished data so as to make this account as complete as possible.

> currant plants which had been previously set out in an isolated garden for the purpose. After inoculation the plants were covered for two days by a box having a glass lid. In all cases, water was sprinkled three or four times daily on the plants and on the inside of the box, to keep a high humidity. Unfortunately, during the whole of the period covered by this series of inoculation the weather was exceedingly hot and dry, and it was evident from a study of field conditions that infections could take place at this time only with the greatest difficulty. The adverse nature of the weather conditions will serve to explain the meager results. . . .
>
> The only positive result from this experiment was that the spores would retain their power of infection for a period of nine days at least; but so many failures occurred all through the course of the work that this period can not be regarded as establishing a maximum limit of life.
>
> It is interesting to note that the spores kept outside underwent a complete decolorization in two days, whereas those stored in the laboratory retained their normal color, with but little change throughout the whole time of the experiment.
>
> The inconclusive results obtained from the first set of inoculations in the field led to another later attempt with plants kept in the laboratory, for this purpose a number of small plants being used from which the leaves had been stripped, so as to induce the formation of secondary foliage. The methods employed in this case were the same as for the first set, exept that after inoculation the shoots were kept covered and moistened for the usual 48 hours inside large glass jars. (See Table IV.)

TABLE IV.—*Inoculation of currants with uredospores of different ages.*

Series.	Age of spores (days).	Date of inoculation, 1916.	Number of leaves used.	Date of examination, 1916.	Result.
I	2	August 31	16	September 19	5 pustules on 2 leaves.
II	4	September 2	16	September 22	67 pustules on 11 leaves.
III	7	September 5	16	September 25	No infection.
IV	8	September 6	14	September 26	10 pustules on 5 leaves.
V	11	September 9	11	September 29	8 pustules on 2 leaves.
VI	13	September 11	16	October 1	2 pustules on 2 leaves.
VII	18	September 16	5	October 6	No infection.
VIII	24	September 22	7	October 12	Do.
IX	27	September 25	7	October 15	Do.
X	31	September 29	7	October 19	Do.

> The results from these inoculations were somewhat better than those from the first set; infections were obtained from spores kept for 13 days after collection, as shown in the tabulated record. It is still thought that this period is far below the maximum period for which the spores will retain their vitality.

In 1917 Gravatt and Taylor made a series of tests of urediniospores together with æciospores and teliospores. (See p. 38 for details of the experiment.) They were tested weekly beginning May 8. June 16 gave the last germination in lot A, while lot B persisted until July 2. Although germination persisted longer in lot B, it weakened decidedly somewhat earlier and was poorer practically throughout the test. (See Table II, p. 38.)

In 1918, Duff (30) experimented on the longevity of urediniospores placed in a refrigerator at 2° to 5° C. two weeks after collection and tested in hanging drops of distilled water. He states that when placed in the refrigerator—

> A negligible percentage of spores were germinable, but reduction in temperature stimulated them to greatly increased germination. By this means a continually

decreasing percentage of spores were kept in a viable condition, until after a lapse of a further period of about three weeks the number that germinated readily was negligible once more. Before the end of four weeks the spores had ceased to germinate.

Extensive tests of the longevity of urediniospores were made by York, Overholts, and Taylor.[40] In one experiment leaves of *Ribes nigrum*, *R. vulgare*, and *R. reclinatum* were placed in bags of mosquito netting with the urediniospores outward. The bags were placed on three stakes at 6-inch intervals, the lowest one touching the ground and the highest 5 feet above the soil. The lowest spores remained viable only 6 to 9 days, while the upper ones were viable longest, 65 days. A 2-day rain began the day after starting the experiment and again a 1-day rain two days later. The urediniospores from *R. nigrum* remained viable longest. Again infected leaves of *Ribes nigrum*, *R. vulgare*, *R. cynosbati*, and *R. glandulosum* were put in open boxes and exposed for 4 hours to the early morning sun. Viability persisted only 15 days. The urediniospores from *Ribes nigrum* remained viable longest. Urediniospores on pulled bushes of *Ribes glandulosum* and *R. cynosbati* hung in the bright sun remained viable only 4 days. Spores on leaves of *Ribes nigrum* dried in a plant press, then put in tight Mason jars and stored in an ice-box remained viable 80 days. Successful inoculations were made with urediniospores collected 270 days previously and also with urediniospores from dead, overwintered leaves of the previous season. The age of the spores is not known, but they were certainly overwintered spores (180). It was found that viability in tap water persisted at least 169 days when the spore-bearing leaves were air dried and kept under slight pressure between sheets of heavy glazed paper. When kept out of doors but protected from rain, they retained viability for 100 days.

In 1918 Pennington[41] made a number of tests of the longevity of urediniospores. In July and August urediniospores on Ribes leaves brought into the laboratory and air dried lost their viability within a week when tested in drop cultures of tap water. On September 25 many Ribes leaves were collected and allowed to dry between sheets of paper. The second day urediniospores from these leaves gave 50 per cent germination when tested as above. The leaves were left in the dry air of the laboratory. The spores decreased in viability until November 26 when but 1 per cent germinated. After that there was no germination.

These results, showing a longevity ranging from 7 to 270 days under varying conditions, indicate the sensitiveness of the urediniospores to external factors. In addition it is quite possible that the physiological condition of the host plant also has a profound effect upon these spores.

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[40] York, H. H., Overholts, L. O., and Taylor, M. W. The longevity of the sporidia of Cornartium ribicola. Seen in manuscript. To be published in Phytopathology.

[41] Pennington, L. H. Op. cit.

THE TELIA AND TELIOSPORES.

GENERATIONS OF TELIA.

In 1918 Pennington [42] made observations upon the generations of telia at Lewis, N. Y. This was a season very favorable for the occurrence of distinct waves of spore production. The first generation of telia appeared on June 28 with and following the second crop of uredinia. They were present throughout the rest of the season, but in the greatest abundance with and immediately following a new generation of uredinia. As compared with the uredinia, they were produced in relatively greater abundance with each succeeding generation. There were six distinct waves of telial production.

SEASON OF PRODUCTION OF THE TELIA.

The date when the first telia are produced varies from year to year with the earliness of the season. The earliest of which we have definite record is June 2, 1918, at North Conway, N. H. Table V (p. 72) gives data for the different regions of North America. The telia are formed until the Ribes leaves fall in the autumn. Drought is likely to cause premature shedding of diseased Ribes leaves soon after the first telia form. This greatly limits the production of new telia.

DISTRIBUTION OF THE TELIOSPORES.

Because the teliospores are produced in more or less compact columellæ they are normally not separated from the host plant. They do become distributed somewhat, however. Gravatt and Marshall (45) found that slugs eat telial columns from rusted Ribes leaves; also that sow bugs carry broken columns on their bodies. There seems to be no reason why insects and other animals may not do likewise.

The telia are sometimes mechanically broken off and blown about by the wind.

Diseased Ribes leaves fall to the ground and are blown about by the wind. Often they are broken into small pieces which may be blown long distances. In fact, York [43] found such bits of dead leaves in his spore traps 200 feet distant from the nearest Ribes bush. Telia on dead leaves kept out of doors in the shade are known to retain viability for 65 days, so that in this way the disease might appear in very unexpected places on pines at a greater distance than the sporidia are carried in a viable condition.

GERMINATION OF THE TELIOSPORES.

The teliospores germinate readily in tap water and produce sporidia in 6 to 12 hours.[43,44] Each spore produces normally a 4-celled pro-

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[42] Pennington, L. H. Op. cit.

[43] York, H. H. Op. cit.

[44] York, H. H., Overholts, L. O., and Taylor, M. W. Op. cit.

mycelium. Each cell regularly puts forth a stout sterigma on which the very thin walled, globular sporidium soon develops. The sporidium has a tiny papillalike swelling where it was attached to the sterigma. The sporidia are 8 to 10 microns in diameter (20). The germ tubes of the teliospores, if developed under water, may not form promycelia but extend elongated hyphæ (20). Under favorable conditions a high percentage of the teliospores may germinate, but because of their aggregation into columellæ it is impossible to make an exact count of the germinating spores. Cooling on ice stimulates viability markedly.

LONGEVITY OF THE TELIOSPORES.

The longevity of the teliospores of *Cronartium ribicola* does not seem to have received as much attention as that of the æciospores and urediniospores. Gravatt and Taylor made tests with teliospores in 1917 similar to those described as made by them with æciospores and urediniospores. (See Table II.) Weekly tests showed that germination persisted in lot B 35 days, while it lasted 56 days in lot A. Saprophytic fungi attacked the lot kept on the window sill, so that the test probably does not show the longevity of healthy teliospores.

York[45] in 1918 found that teliospores were still capable of germination in tap water after being kept on the plucked leaves 65 days out of doors in the shade. A similar test of teliospores kept in the dark in the laboratory gave germination for 90 days.

THE SPORIDIA.

SEASON OF PRODUCTION OF THE SPORIDIA.

The sporidia may be produced as soon as the telium is mature, if there is sufficient moisture in the air for a number of hours.

The telia may remain alive on dry dead leaves out of doors for more than 65 days, so that sporidia might be produced well into the winter in mild seasons, thus prolonging the danger season for pines.

DISTANCE OF DISSEMINATION OF THE SPORIDIA.

In work with spore traps by Pennington[46] and Snell in 1918, sporidia were caught up to 60 feet from very heavily infected Ribes bushes. This was in the eastern Adirondacks, about 8 miles from Lake Champlain. Hundreds of pines were examined for infections. In no case was infection found on pines as far as 200 feet from Ribes plants. Pennington made a study of nine outbreaks in pines in the Adirondacks. The infection on pines was confined to an area within 100 to 200 feet of the Ribes plants which infected the pines.

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[45] York, H. H. Op. cit.

[46] Pennington, L. H. Op. cit.

In 1919, Pennington (cited in Spaulding, 146) caught sporidia up to 294 feet distant, but they failed to germinate. Under favorable conditions, sporidia caught at a distance of 177 feet germinated, but none beyond this distance.

York,[47] working in the White Mountain region of New Hampshire, in 1918, found that sporidia were quite common in spore traps exposed 24 hours at a distance of 200 feet from the diseased Ribes bush. York (cited in Spaulding, 146) in 1919 caught sporidia, under favorable conditions, at 600 feet distance, which germinated.

The infection of pines is said by McCubbin (88) to depend on "(1) The nearness of cultivated Ribes, particularly black currants; (2) the number of wild Ribes present; (3) the moistness of the situation." York [47] concluded that these factors are "topographical features, direction of the wind when sporidia are produced, humidity of the air, precipitation, and the nature and density of vetegation between the Ribes and pines." Pennington [48] stated that weather conditions have much to do with the degree of infection that occurs on pines; cool, moist situations favor infection; intervening barriers of vegetation tend to limit infection; the amount of infection under given conditions varies directly as the extent of Ribes leaf surface and inversely as the square of the distance from Ribes. The writer (145) said the width of the Ribes-free zone around pines is largely to be governed by topographical features; direction of the wind prevailing at the time the sporidia are produced; humidity; age of the pines; exposure and species of Ribes; and the composition, height, and density of the vegetation between the Ribes plants and the pines. The experiments with the sporidia show that high humidity is necessary for these spores to live any length of time. It alone may very largely determine whether infection can take place.

A few specific instances show the effect of these factors in actual outbreaks. On July 10, 1917, on Gerrish Island, at Kittery Point, Me., Gravatt investigated the small trees of *Pinus strobus* within a radius of 15 feet of a bush of *Ribes hirtellum* to determine the spread of infection. The gooseberry was a small bush, having approximately 270 small leaves and there were no other Ribes near by to influence the result on pines. The ages of the pines were as follows: Two years, 12; 3 years, 17; and 5 years, 82; a total of 128 pines, none over 5 years of age. There were 77 separate infections on 54 diseased trees, 44 of these infections being on 2-year wood. As the oldest pines were 5 years old and most of the infections which occurred the year before were probably not detected, this infection of more than 40 per cent resulted from an exposure of only a little more than

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[47] York, H. H. Op. cit.

[48] Pennington, L. H. Op. cit.

3 years to the disease. To judge from the results of the first five years, it is not likely that any of the pines within the 15-foot radius would remain alive at the end of 12 or 15 years. Pines outside the 15-foot radius from the bush showed only scattering infections. This was in a location well protected from strong winds.

In another case where *Ribes nigrum* was well exposed to the strong storm wind from the neighboring White Mountains, York found pine infections up to 600 yeards distant from heavily diseased Ribes bushes.[49]

In the outbreak at Kittery Point, Me., Posey found that a number of *Ribes nigrum* bushes so located that the wind had moderate access to them caused infection of *Pinus strobus* trees up to a distance of about 300 yards.

> Our studies (146) of the distance of distribution of the various spore forms and of the distance that infection has actually occurred upon pines from known infected Ribes indicate that the Ribes-free zone should be, under average conditions, 200 to 300 yards in width. It should be much more where conditions are exceptionally favorable for transfer of the spores from Ribes to pine, i. e., near large bodies of Ribes, where there is no screen of vegetation over the Ribes or between the Ribes and the pines, or in exceptionally humid situations. The cultivated black currant (*Ribes nigrum*) should not be allowed in an infected pine district because of the special danger from it.

Studies by York [49] of the natural infections of pines show that the sporidia are blown along roads cut through heavy forest cover and that they do not reach pines located in isolated small pockets in the dense forest. Trapping of sporidia from Ribes located under dense cover of black alder yielded sporidia only up to a distance of 75 feet. Traps set 20 feet in the air and well above the cover, but directly over the Ribes bushes, caught no sporidia.

AGENTS DISSEMINATING THE SPORIDIA.

It is apparent that the sporidia produced by the teliospores of *Cronartium ribicola* are largely disseminated by the wind. Observations in various areas where white pines have become infected from neighboring Ribes bushes show plainly that this is the case. In such cases the infection is most intense nearest the Ribes bush acting as a center of infection. The degree of infection decreases as the distance from the center increases. Other conditions being equal, the distance of pine infections from the infection center is very short where there is a thick screen over and around that center, while the converse is true where the Ribes infection center is well out in the open. (See pp. 64 to 66 for data bearing on this matter.)

Minor disseminating agents are known, and their number will undoubtedly be increased by future investigations. The investigations of Gravatt and Marshall (45) in the experimental greenhouse

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[49] York, H. H. Op. cit.

at Washington, D. C., showed that weevils, snails, slugs, and sow bugs feed on the telia.. The voided teliospores retained viability in a few instances. This indicated that similar animals might be active agents in the local distribution of these spores out of doors. Investigations by Snell (127) in 1918 at Lewis, N. Y., showed that a number of different types of insects feed on rusted leaves of Ribes bushes and may serve as carriers of the sporidia directly from plant to plant, or indirectly by the voided teliospores. Marshall, in 1917, found that the moist sporidia allowed to dry on a feather are not easily dislodged therefrom, either by wind or by brushing of the feather on cloth. This suggests the possible carriage of sporidia by migrating birds in the fall for long distances. Their very short life, as determined by York (see pp. 67–68), however, probably prevents their causing infection of pines under these conditions.

The remarks on the carriage of æciospores by currents of air generated by fast-moving automobiles, steam trains, and electric cars also apply to the sporidia. (See p. 36.)

GERMINATION OF THE SPORIDIA.

Gravatt, Colley (20), and York, Overholts, and Taylor[50] found that the sporidia germinate immediately in tap water under favorable conditions. They germinate like ordinary fungus conidia, by pushing forth a germ tube which is relatively large. They are capable of germination as soon as they reach full size, even though still attached to the promycelium. The germ tube normally develops until a mycelium is formed. In some cases the germ tube soon forms a secondary sporidium which in turn may germinate. The viability of the fresh sporidia is high, as many as 90 per cent germinating within 24 hours.

LONGEVITY OF THE SPORIDIA.

The sporidia of *Cronartium ribicola* are so thin walled and fragile in character that it seems self-evident that they are short-lived spores. This supposition has been proved to be correct by the work of York and Overholts in the summer and autumn of 1918 and of York and Taylor in 1919 (cited in Spaulding, 146). Colley (20) found in 1917 that fresh sporidia germinated readily in distilled-water cultures. York, Overholts, and Taylor[50] dried the sporidia on glass slides and tested their viability after varying intervals. Very slight germination resulted after 10 minutes exposure by an open window at 66° F. when light rain was falling. None survived when exposed to bright sunlight for 10 minutes with a temperature of 77° F. Nor did they survive when pieces of Ribes leaves bearing the telia and sporidia were exposed to sunlight for 10 minutes at 85° F. and with a humidity

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[50] York, H. H., Overholts, L. O., and Taylor, M. W. Op. cit.

of 30.5 per cent. In another experiment the sporidia were placed on the periderm of white-pine twigs of the same season's growth and on living leaves of *Pinus strobus* and *P. rigida*. They were then exposed dry at 66° F. and with a humidity of 90 per cent. None survived for 10 minutes. At 72° F. and a humidity of 69 per cent none survived for 10 minutes. They conclude that the sporidia can endure very little desiccation and are short lived under seemingly optimum conditions. Abundant moisture is necessary for infection of pines to occur.

HETERŒCISM OF THE SPORIDIA.

A number of tests have been made to learn whether Ribes might become infected by sporidia of *Cronartium ribicola*. Jaczewski (59) states that experiments have shown that they will not infect Ribes leaves. In 1913, Clinton, Stewart, and the writer (151) inoculated *Ribes nigrum* leaves with teliospores overwintered out of doors, but there were no infections. In 1912 the writer tested fresh teliospores without infection occurring (136). In 1917 Gravatt made several tests of fresh, sporidia-producing telia, but no infection resulted.

OVERWINTERING OF CRONARTIUM RIBICOLA.

Overwintering on Pines.

The generally accepted view has been that *Cronartium ribicola* lives over winter by means of the mycelium in the bark of living infected pines and by this means only (142). A number of writers have mentioned cases where their observations seemed to indicate the possible overwintering on infected Ribes, but nothing that could be accepted as real evidence was offered until the last few years. There is no question that the fungus overwinters chiefly in the infected living pine trees and has been carried in the dormant condition from continent to continent in young infected pines.

It has been discovered, as has been mentioned earlier, that *Cronartium ribicola* may overwinter as mycelium in infected branches cut from diseased trees late in the fall, or during the winter, and allowed to lie until spring. Then, if these cut-off branches lie close to damp soil or with the cut ends in a stream or pool, fresh vigorous æcia are produced (89). Still another phase of overwintering was discovered by Dosdall (29) in Minnesota. On April 19, 1918, a dead branch of white pine, bearing an infection which bore æcia in 1917, was collected. Germination tests in distilled water showed that 1 to 2 per cent of the old æciospores were still viable.

Overwintering on Ribes Plants.

Investigations of overwintering of *Cronartium ribicola* on Ribes plants, in Europe, seem to be limited to field observations. They relate to instances where diseased Ribes bushes were found widely separated from *Pinus strobus* or from all 5-leaved pines (6). These necessarily depend for reliability upon the observer's complete and minute knowledge of the Ribes and pines within considerable areas. Hence, such observations are of very uncertain value. Investigations showing that the æciospores of this fungus are distributed for miles largely invalidate such observations so far as overwintering is concerned.

In North America, investigations of overwintering on Ribes plants have been along the following lines: (1) By means of spores adhering to dormant Ribes plants, (2) in dormant or partially opened Ribes buds, (3) in living Ribes leaves which themselves lived over winter, (4) on dead Ribes leaves, and (5) on infected Ribes stems.

Overwintering by means of spores adhering to dormant Ribes plants has been investigated in several ways. A great many field observations have been made upon bushes diseased heavily one year and not infected the succeeding year. Cases where bushes were shipped from known diseased localities and have shown the rust the next season in their new locations, have been considered, but the evidence has been too incomplete to be seriously considered except as it might help to confirm or refute other stronger evidence. A great many Ribes plants have been used by the writer in greenhouse experiments; they shed their leaves and become dormant for several months, yet there has been no hint of the carrying over of the fungus upon them from one season to the next. A cooperative experiment was made with Stewart (151), using 500 plants of *Ribes nigrum*, which in the summer of 1912 were heavily infected. The leaves dropped normally. They were then dug and most of them heeled in out of doors until February, 1913. They were then brought into greenhouses in six widely separated localities and allowed to put forth new leaves. Examination of some of these dormant plants by Arthur and Petry showed that plenty of urediniospores still adhered to the stems and buds. Inoculations with these spores did not give any infection, so that they presumably had lost their viability. The results reported by six different investigators showed no infection appearing on the new leaves.

Howitt and McCubbin (56) in attempting to solve the overwintering problem, made the following tests:

> (1) In the fall of 1914, 16 black and 7 red currant bushes and 1 gooseberry bush, all badly rusted, were stripped of leaves and placed in cold storage, where they remained until March 16, 1915. At this date they were removed and planted in a greenhouse. All grew well and produced healthy leaves and fruit and were entirely free from rust throughout the summer. In addition, 17 black currant bushes, which had been badly rusted in 1914 and which were wintered in the field, were added to the above on April 21, 1915. These also grew normally and without rust.

(2) Seventy-eight black currant bushes, badly rusted in 1914 were wintered in the nursery rows, and transplanted April 12, in various gardens, isolated as far as possible from infected white pines and currants. These were inspected six times during the summer, the last inspection being made on October 2. At this date all were still free from rust except two bushes, on each of which a few rusted leaves were found. There is reason, however, to suspect that these infections might have been due to spores carried from currants about a mile distant from the garden in which they occurred. In no case was rust found on any of these currants which were located more than a mile from a source of infection.

(3) A number of bushes from the same source as No. 2 were planted in five lots in a region known from personal observation to have been entirely free from the rust in 1914, and which is 60 miles from the nearest known source of infection. Of the 100 bushes set out here only one developed rust, and this late in the season. All conceivable sources for this infection have been accounted for except two, viz, the wintering over of the rust on the currant itself, or accidental infection from spores carried on the writer's clothing while making an inspection on May 24.

In 1917, V. B. Stewart (152) tested the possible overwintering of the fungus by means of spores adhering to diseased bushes of *Ribes nigrum*. These were heavily infected in 1915 and 1916. In August, 1916, they were defoliated, and 200 were dug and placed in a storage cellar in October, where they remained all winter. In 1917, they were sent to Ithaca, N. Y., and set out in a field. The disease had not been known within 40 miles. The disease did not appear upon them up to October 9, 1917.

The possibility of overwintering in Ribes buds was brought to the writer's attention by infections of petioles (131, 134, 135), by which means it seemed entirely possible for the mycelium to travel from a leaf blade down the petiole and thence into the stem and bud in the axil of the leaf. While many diseased petioles have been examined, no indication of the migration of the hyphæ into the stem or bud has yet been seen. Direct examination of buds on heavily infected bushes has also failed to yield any indication of bud-scale infection (151). McCubbin (85) suggested but could not prove that infection of partially opened buds late in the fall might result in some of the infected leaflets surviving the winter and developing the disease the next spring. York[51] successfully inoculated the inner bud scales of opening buds of *Ribes nigrum* with æciospores, suggesting overwintering in this way.

The possibility of green leaves living over winter on Ribes plants out of doors has been investigated. In three cases, the writer had Ribes plants growing in pots plunged in sand out of doors at Washington, D. C., retain green leaves through the winter until the spring weather of March, 1918, set in. One plant of Cumberland gooseberry and two plants of Utah Yellow currants did this. They were taken as specimens on March 22, when warmer weather set in. The

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[51] York, H. H. Op. cit.

previous winter a single seedling plant of an unknown species bore leaves flat on the soil under similar conditions until March 12, 1917, when it was brought into the greenhouse and inoculated. It promptly took the disease on the overwintered leaves. York [52] found *Ribes glandulosum* plants in the spring of 1918 which bore overwintered leaves that later became infected naturally. In such cases, it would be easy to understand that late infections in the fall might lie dormant until spring and then produce vigorous uredinia. More time is necessary to determine whether this actually occurs.

As stated previously, infection of petioles by *Cronartium ribicola* is quite common. Early in 1917 Colley (17) discovered that infected petioles often had telia and masses of active mycelium as well as uredinia in the central pith. This raised the question of the possibility of such mycelium remaining active until spring and producing new uredinia.

Whether the fungus can live over winter on dead diseased leaves seemed unlikely in view of the negative results of Arthur and Petry (151) with urediniospores from stems of plants diseased the preceding summer, and the negative results of Stewart (151) with material overwintered out of doors at Geneva, N. Y. Howitt and McCubbin (56) early in 1915 attempted to produce infection by spores which remained over winter out of doors on dead Ribes leaves. All of their attempts were unsuccessful. In the spring of 1918 York (180) and the writer obtained infections with urediniospores overwintered out of doors in Massachusetts on dead Ribes leaves, proving that urediniospores may survive the winter. This was repeated in the spring of 1919 by Taylor (157).

The possibility of infection on Ribes stems was early investigated by the writer but with no success. Many inoculations were made on young Ribes shoots by the writer and later by Gravatt, Doran (28), and York [52] but without success. However, in the summer of 1917, Posey and Gravatt (112) discovered fruiting uredinia on the young shoots of *Ribes hirtellum* at Kittery Point, Me. They inoculated other young shoots with æciospores and secured mature uredinia. Colley found uredinia in the pith of these infected stems. Gravatt later inoculated young seedlings of *Ribes fasciculatum* in the greenhouse with æciospores and secured heavy infection of the cotyledons. In one seedling the fungus also attacked the stem just below the diseased cotyledons and developed several uredinia (Pl. V, fig. 2). Later, however, the plant outgrew the disease. Taylor and York have successfully inoculated stems of several species of Ribes. (See p. 50.)

That *Cronartium ribicola* overwinters on Ribes is established.

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[52] York, H. H. Op. cit.

IMPORTANT DATES IN THE LIFE HISTORY OF CRONARTIUM RIBICOLA.

Table V shows some of the more important dates in the development of the white-pine blister rust and their variation according to locality. These dates are rarely the earliest or latest possible ones, but are based upon notes actually made respecting the point covered. It is hoped to extend this table greatly and approach nearer the actual date when each stage of development is reached by the fungus in the various regions. Southern New England is here made to include Massachusetts, Connecticut, and Rhode Island. Northern New York is understood to include approximately that part of the State lying north of a line between Glens Falls and Oswego. The Lake States include Michigan, Wisconsin, and Minnesota. Similar data for Europe are given in the last columns of the table for the sake of comparison.

TABLE V.—*Important dates in the life history of Cronartium ribicola, as observed in America and in Europe.*[a]

[To economize space, the century digits 19 are omitted in noting the year of each observation; thus '09=1909.]

Development noted.	United States.					Europe.	
	Southern New England.	Southern New York, New Jersey, and eastern Pennsylvania.	Northern New England.	Northern New York.	Lake States.	Date.	Locality.[b]
First closed blisters	Apr. 7,'17	Apr. 30,'11	Apr. 15,'10	Apr. 26,'18	May 5,'17	Apr. 16,'90	H
	Apr. 5,'18	Apr. 28,'17	Apr. 7,'17	Apr. 21,'19	Apr. 19,'18	Apr. 15,'01	M
		May 4,'18	May 13,'18		Apr. 18,'19	Apr. 7,'09	D
						Mar. 17,'18	F
First open blisters	June 22,'09	June 1,'09	June 14,'09	June 8,'09	May 24,'16	Apr. 15,'90	H Bo
	May 22,'11	July 27,'10	May 26,'10	May 12,'10	May 8,'17		
	May 16,'12	May 5,'11	June 9,'11	Apr. 26,'18	Apr. 19,'18	Apr. 29,'96	S
	June 3,'13	June 10,'13	May 15,'12	Apr. 23,'19	Apr. 22,'19	Apr. 28,'08	B
	May 25,'14	May 20,'15	June 6,'13				
	June 2,'15	Apr. 7,'16	May 15,'15				
	May 3,'16	Apr. 28,'17	May 15,'16				
	Apr. 17,'17	May 16,'18	Apr. 29,'17				
	Apr. 7,'18		Apr. 23,'18				
	Mar. 28,'19		Apr. 7,'19				
Last yellow blisters			June 7,'10	June 12,'18	June 24,'17	May 15	H
			July 1,'17	June 26,'19	June 24,'19	May 9	D
			July 21,'18		Sept. 16,'19[c]	June 1	Bo
						May 19,'18	F
First uredinia	June 3,'16	June 10,'13	July 24,'13	July 25,'09	June 9,'16	May 23	D
	June 13,'17	July 18,'16	July 14,'14	July 18,'16	June 12,'17	May 30	B
	May 29,'18		May 20,'17	June 28,'17	May 18,'18	May 26	B
			May 16,'18	May 16,'18	June 5,'19	June 2,'19	S
			May 23,'19	May 23,'19			
First telia	June 17,'16		June 26,'13	Aug. 23,'17	July 21,'16	Aug. 1	B
	July 21,'17		July 24,'16	June 26,'18	June 12,'17	July 30	M S
	June 19,'18		June 10,'17	June 30,'19	July 8,'18		
	July 30,'19		June 2,'18		July 10,'19		
			June 6,'19				
First pycnial drops	June 21,'16		July 26,'13	July 3,'18		June	H
	June 7,'18		June 7,'18	June 26,'19			

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[a] Notations for Ontario, Canada: First open blisters—May 10, 1917, and June 22, 1918; first uredinia—June 24, 1915, and July 20, 1916; first telia—June 24, 1915.

[b] Abbreviations used: B=Berlin, Bo=Bohemia, D=Denmark, F=France, H=Hamburg, M=Munich, S=Silesia.

[c] This date is an extraordinarily late one for æcia to be formed, but it is included here to show the possibility of the æcial season being prolonged throughout the summer.

CONTROL OF THE WHITE-PINE BLISTER RUST.

Significant Factors Which Determine Control.

FACTORS IN THE FUNGUS.

The significant features in the life history of *Cronartium ribicola* are as follows: The pycnospores are apparently functionless; the æciospores are not known to infect pines, but they do infect Ribes readily; the urediniospores are not known to infect pines, but they do infect Ribes; the sporidia produced by the teliospores are not known to infect Ribes, but they do infect pines.

The spores are all distributed by the wind much more than by any other agency. The æciospores are carried and are capable of infecting Ribes leaves miles away from their source. The urediniospores are distributed a number of hundred yards, but appear to lose their viability soon, so that infection by them is rather limited in extent. The sporidia produced by the teliospores appear to be distributed to a distance of a few hundred yards, but they are so frail that they soon lose viability. Infection by them is limited to 100 to 600 yards as a general thing, and more commonly the former than the latter distance.

The fungus lives over winter most commonly by means of the mycelium, presumably in the needles and certainly in the bark of infected white pines. It occasionally overwinters by means of the æciospores in cankers of pine bark or by the urediniospores on Ribes leaves. The æciospores produced by the overwintered mycelium in the pine bark are the principal source of infection of the Ribes leaves each spring. The æciospores carry the disease far and wide for miles to the new Ribes leaves. The urediniospores intensify the disease in the vicinity where it is started by the æciospores. The sporidia carry the disease back to those pines which are relatively near infected Ribes bushes.

High humidity of the air is necessary for any of the spore forms to germinate and to produce infection.

FACTORS IN THE ENVIRONMENT.

CLIMATIC FACTORS.

Climate may be reduced to the three most potent factors—moisture, sunshine, and wind. *Cronartium ribicola* is absolutely dependent upon abundant moisture for its development. Drought, especially if prolonged, apparently may hinder the development of the æcia (49, 135). Lack of moisture prevents germination of all the different forms of spores. It prevents or very greatly reduces the extent of infection on Ribes plants by æciospores. It prevents the production of new generations of urediniospores,[53] and consequently prevents the abundant formation of uredinia as well as

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[53] Pennington, L. H. Op. cit.

restricts the spread of this stage of the fungus. Moreover, drought very largely reduces viability of the urediniospores.[54] With the very short-lived sporidia of the teliospores it is evident that lack of moisture immediately after their production may entirely prevent their infecting pines at all, and drought is known greatly to limit their formation. Drought causes the premature fall of leaves of Ribes bushes so as to leave practically nothing for the fungus to subsist upon late in the season. Thus the crop of teliospores is so greatly reduced in times of drought that infection of pines is largely or entirely prevented. Drought kills many young Ribes seedlings and many are winterkilled (23, p. 8). On the other hand, rain undoubtedly beats down the spores floating in the air and washes spores from the host plants, so that infection by them is prevented.

Sunshine, by influencing the moisture of the air, may be very potent in reducing the activities of the fungus. It has a direct deleterious effect upon the spores[54] (30, 88). It is an open question whether the erratic germination of the urediniospores is not due to this action of the sun's rays. By promoting the quick maturity and hardening of the leaves of Ribes in the open, bright sunlight may greatly reduce the infection which develops upon them.

Wind is apparently the chief agent disseminating all forms of spores of this fungus. Its activity greatly influences the spread of the disease.

THE AGENCY OF MAN.

Man is a most potent agent in the dissemination of the white-pine blister rust. Through his activities it has made all of its known long-distance jumps. There is reason to believe that it is a native of northern Asia, whence it spread to Europe. The extensive trade in young trees of *Pinus strobus* is known to have been the means of introduction of this disease to many parts of Europe (111, 120, 155, 162, 170). It certainly came to North America in young white-pine stock from Europe and has attained its present wide distribution here in such imported stock. See figures 2 to 12, showing the progress of the disease since 1909.

INSECTS AND OTHER ANIMAL FACTORS.

Various animals (insects, snails, mammals, man, etc.) may aid in the distribution of the disease by carrying spores on their bodies, or they may retard or reduce the fruiting of the fungus by eating the sori on both pines and Ribes; and others such as gipsy-moth larvæ, other insects, snails, and squirrels may even eat the surrounding bark on pines, so that no more sori can form. (Pl. III.) In 1918, Pennington[54] estimated that the production of æciospores in the Adirondacks

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[54] Pennington, L. H. Op. cit.

was reduced about 15 per cent by the eating of infected bark by mice, squirrels, porcupines, etc. Posey and Gravatt[55] found that squirrels had eaten 17 per cent of the æcia-bearing bark in a given area at Kittery Point, Me., and this is substantially true for the infected forests of that section. The leaf-eating insects and mammals may so reduce the leafage of Ribes plants as to reduce the disease materially in a given locality.

OTHER FUNGOUS FACTORS.

Other fungi are of some importance also. At Kittery Point, Me., Colley (20) and Posey and Gravatt[55] found that secondary fungi work in the pine bark infected by *Cronartium ribicola* in such a way as nearly or entirely to kill out the latter, probably by killing the bark around the cankers so that the blister rust is starved out. This sort of thing is quite general where white pines are generally infected by *Cronartium ribicola*. Very often it appears that the diseased pines are killed finally by the secondary fungi rather than by the blister rust. The æcia of *Cronartium ribicola* are sometimes attacked directly by other fungi (80, 168, 172). It has also been found that the uredinia and telia are attacked by various fungi, so that their efficiency is greatly reduced locally (116). Fungi parasitic upon the leaves of *Ribes* sp., causing their premature fall, may greatly reduce the leafage available for the blister-rust fungus to attack and thus reduce the quantity of teliospores to produce infection on pines.

FACTORS IN THE HOSTS.

There are certain factors in the hosts themselves which are important in the control of this disease where it has once become established. These are resistance by some of the hosts to the disease and the natural suppression of the lower branches of white pines.

Among the white pines the blister rust attacks *Pinus strobus* with especial virulence. It does not attack *P. cembra* nearly so readily. Experience shows that *P. flexilis*[56] is decidedly susceptible to it. This is confirmed by Moir's studies in Sweden. Knowledge of the relative susceptibility of the pines is extremely limited, because the disease has been in North America too short a time and has not yet reached any but the eastern white pine. In Europe, where the older outbreaks have occurred, there undoubtedly is an opportunity to obtain definite data on the relative susceptibility of the pines. It may prove feasible ultimately to plant another species of white pine which is not nearly so susceptible to the blister rust and which also is of value as a timber tree.

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[55] Posey, G. B., and Gravatt, G. F. Field studies on the white-pine blister rust at Kittery Point, Me. Seen in manuscript.

[56] Pennington, L. H., Snell, W. H., York, H. H., and Spaulding, P. Investigations of Cronartium ribicola in 1920. Seen in manuscript. Published in Phytopathology, v. 11, p. 170–172. 1921.

It has been possible to learn a little more concerning resistant species and varieties of Ribes. *Ribes alpinum* is found to be immune in America, although it is stated that it takes the blister rust in Europe. There does not appear to be any resistant species which will take the place of the cultivated *R. nigrum* (the black currant), or of *R. odoratum* (*aureum*) (the flowering currant). Among the cultivated red currants the varieties Franco-German, London, Rivers, and Holland have shown themselves very resistant. In generally infected areas these may prove of value to replace the more susceptible varieties.

In the outbreak area at Kittery Point, Me., one of the oldest in North America, the infected pines are thickly crowded together and mostly range in height from 15 feet upward. The lower branches are being suppressed and are dying rapidly from overcrowding. Experience has shown that trees and branches attacked by the blister rust are weaker than healthy ones and are more apt to die from drought and suppression. Posey and Gravatt[57] find that this natural suppression of lower branches at Kittery Point has resulted in the killing of many entire branches bearing blister-rust cankers well out from the trunk of the tree. In such cases the disease in the dead branches is killed also. They find that about 15 per cent of the trees originally infected have thus recovered from the disease before it reached their trunks. As above intimated, this process is probably at its height in this area, since suppression of the branches is apparently at its maximum.

Experiments in Control in Europe.

In experimenting with the white-pine blister rust, the European investigator has always had a different viewpoint from that of the investigator in North America. This has been due to two reasons—the disease was possibly native in Europe, certainly in Asia, but was introduced into North America; *Pinus strobus*, the favorite pine host for the fungus, is native in North America and introduced into Europe. That is, the situation is exactly reversed in every respect in North America as compared with Europe.

The disease is generally considered to have been native in the Alps and in the Ural Mountains upon *Pinus cembra*. It appeared in widely separated localities through Northern Europe before plant pathology had developed to any extent. That is, organized quarantines, present methods of spraying, and many other methods now used in fighting plant diseases were unknown at that time. The fact that the disease was prevalent practically throughout northern Europe before it became generally known, showed plainly that it was firmly established throughout that region. This meant that

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[57] Posey, G. B., and Gravatt, G. F. Op. cit.

eradication was impossible. Local control has therefore been the only aim of the Europeans. Besides all this, the application of methods of control to plant diseases in Europe has never been developed to such a point as it has in North America except for relatively few diseases of the more important cultivated crops. There has apparently never been a well-planned investigation of the control of this disease extending over a number of years anywhere in Europe. All European publications upon control are fragmentary. It is evident that many scattered efforts have been made to control the disease there, but the results have never been published.

As stated above, the status of *Pinus strobus* in Europe is entirely different from its status in North America. While it has been more than 200 years since it was introduced into Europe (5), it of course has not approached the distribution that a tree does in its native region. It has been widely distributed in Europe as a park and ornamental tree and has been very popular for this purpose. As a forest tree it is a species which is planted in relatively small blocks and even then only on an experimental scale. In Europe it is essentially an ornamental tree rather than an important timber tree. Its total value there is exceedingly small compared to its total value in North America.

Legislation against plant diseases in Europe is so complicated that no attempt will be made here to give an outline of it. Incidentally, it should be stated that Tubeuf (162, 163, 164, 169, 170, 174) has repeatedly called attention to the fact that commercial nurseries have been and are still spreading this disease throughout Germany. In 1904 he (170) repeats earlier demands for a national control of the forest-tree nursery trade and goes so far as to refute the statements of Schwarz (125) that this disease in the nurseries at Halstenbek is absent or negligible. It is evident that the nursery trade dominated the situation and prevented such action.

Since the disease on Ribes plants is essentially one of the leaves, there has been an apparent chance for success by spraying them. Tubeuf (165) seems to have been the first to report on such tests. He sprayed Ribes leaves in the greenhouse with Bordeaux mixture and then set the sprayed plants among those already diseased. Numerous uredinia soon developed on the lower sides of the sprayed leaves. Jaczewski (58) says that spraying with Bordeaux mixture is not very effective.

Ewert (37) in 1912, to prove whether infection of Ribes leaves always occurs on the lower side only, made a test on a bush of *Ribes nigrum*. This bush was one of a number of Ribes plants upon which *Cronartium ribicola* had appeared every year for a decade. One-half of the bush was sprayed on the lower sides of the leaves only; the other half was untreated. Spraying was done on March 28, April 9 and 27, May 3, 7, and 20, June 1, and July 9. About 1,000 leaves were borne on the bush on June 27 so that each half had approximately 500 leaves. At that time the unsprayed half had about 250 leaves so heavily infected on the lower surface that some were already about to fall. On the sprayed half only 10 leaves were infected, all but one of these had only 1 or 2 sori, a single leaf had more. In this season the fungus attacked all the Ribes bushes very heavily, more so than for 10 years preceding.

It is noted that Ewert does not say specifically that sori formed only on the lower surface of the leaves. They may be presumed to have done so.

On April 26, 1913, Ewert placed four potted plants each of *Ribes nigrum*, *R. aureum*, and *R. rubrum* (var. Red Holland) around a tree of *Pinus strobus* heavily infected with *Cronartium ribicola*. On April 26, May 9, 17, and 24, June 6 and 21, and August 3, the several plants of each species were treated as follows:

Plant 1, sprayed with 1 per cent Bordeaux mixture on only the upper surfaces of the leaves.

Plant 2, sprayed with 1 per cent Bordeaux mixture on only the lower surfaces of the leaves.

Plant 3, sprayed with 1 per cent Bordeaux mixture on both surfaces of the leaves.

Plant 4, untreated check plant.

The checks on May 17 had two leaves with a considerable number of uredinia; on May 25 almost all leaves bore uredinia; and on July 28 there were 50 heavily infected leaves.

Plants numbered 1 (sprayed on the upper surfaces only) on May 25, showed the first uredinia on one leaf; on June 3 six leaves were infected, two very heavily; on July 28 there were 50 infected leaves.

Plants numbered 2 (sprayed on the lower surfaces only) on June 3 first showed very slight infection on two leaves; on July 28 four leaves were infected, all lightly.

Plants numbered 3 (sprayed on both upper and lower surfaces) on July 24 were healthy. On June 28 one leaf bore a single uredinium.

Here again Ewert fails to state definitely whether or not the infections were all on the lower surface of the leaves.

Ewert's experiment of 1912, spraying one-half of a *Ribes nigrum* bush, was repeated in 1913. In this case the sprayed leaves remained healthy, except where they were not thoroughly reached with the spray. This exception seems to the writer to be significant, as it indicates that spraying carefully enough to control the disease was apparently not practicable even for as painstaking an experimenter as Ewert showed himself to be in planning and carrying out these tests. In 1912 the disease was very virulent, while in 1913 it was not. This probably largely explains the better showing made in 1913 in these experiments. Although spraying greatly reduced the number of uredinia, it did not entirely prevent their formation.

The spraying of pines with fungicides apparently has not received much attention. It is reported that the infection of young seedlings of white pine has been controlled by spraying in Belgium (106).

Pines have been treated in Europe by the application of various chemicals, but the following cases are the only ones where results are given.

Hostermann (55) treated the affected parts of two *Pinus strobus* trees with 10 per cent and 20 per cent solutions of carbolineum. This was applied with a brush on April 28, 1908, before the æcia matured, and again on May 12 and 18. The next spring, æcia started to develop, and the treatment was repeated with a 50 per cent solution of carbolineum. The tree was apparently unhurt, but in the spring of 1910 the fungus was still alive.

In another case (102), where 15-year-old trees were badly attacked on the trunk and the leaves had turned noticeably yellow, the bark was scraped off and the area bandaged with "carbolineum avenarius." A second tree was scraped and a 10 per cent solution of potassium permanganate applied. On a third tree a 1 per cent solution of copper sulphate was used. The first and second trees recovered and the last one died.

Büttner (9) treated 18-year-old *Pinus monticola* trees which had trunk infections. Attempts at cutting out the infections failed. He then applied "tree wax" to the visible infection itself and 20 cm. above and below it. The trees showed no blister rust in 1906. It would be interesting to learn if this held true for several years.

Eriksson (33) recommends the use of tar to cover the infections and prevent the distribution of the spores.

Tubeuf (164) says that valuable trees may be saved by cutting out infections and treating with lysol, asphalt, etc., if Ribes are removed for a distance of 50 meters, so that no new infection can occur.

Kneiff (74) removed blisters by frequent wet rubbing. He also used "tree wax" and cloths wet with carbolineum. These hindered the disease, but he says the best way to fight it is the removal and burning of the diseased parts or plants.

Pechon (105) advises burning affected trees and states that treatment with tar and similar substances will not suffice.

Köhler (75) tried cutting out and smearing, but gave up these methods as causing too much injury and even death. He sprayed the trunks with a strong stream of water before the blisters opened in the spring. The blisters disappeared and the trees formed new bark.

Fungi which parasitize *Cronartium ribicola* are not uncommon. Their use in artificial inoculation of infections on pines has been attempted (172, 173, 174), but with little success. There appears to be little prospect for success commensurate with the expense involved.

The separation of the pines from the Ribes plants is the most efficient method of controlling the disease in a given locality. To judge from the frequency of this recommendation for combating the disease in European literature, apparently considerable work of this kind has been done in Europe; but no definite statement of results in specific instances have been found.

The use of screens of another species of tree between Ribes and *Pinus strobus* has been recommended in Europe (131, p. 41). No one has stated the results of such treatment in any given instance, however.

There must be a chance to secure much valuable data on the success or failure of various methods of treatment which have been tested in Europe, but which have never been published. This can only be done by making definite investigations in Europe from the American standpoint. It must be remembered that from the European point of view the white pine is an introduced and comparatively unimportant tree. Its diseases, therefore, are not made the subject of systematic and prolonged study. Many facts of value fundamental to the control of this disease in America can only be determined by the intimate study on the ground of the much older infections of Europe.

Experiments in Control in North America.

In all control of parasitic plant diseases the fundamental thing is to determine the extent and the distribution of the disease to be controlled. The parasitic fungi are so generally distributed by the wind and are so insidious in their spread that they usually have gotten well started before their presence is discovered. Newly discovered imported diseases must be attacked at once or not at all, if eradication is to be accomplished, but more attention should be given to the matter of determining reliably the extent of outbreaks of such diseases. Scouting is a very important part of any disease eradication or control campaign. A well-conducted, intensive, plant-disease survey will do much to aid in determining the status of a new disease.

METHODS USED.

The control of white-pine blister rust has been attempted in North America (1) by means of quarantines of the host plants, (2) by the eradication of advance infections, (3) by the separation of the two hosts, (4) by sanitation, (5) by screening Ribes or pines with other species, (6) by the judicious selection of planting sites for pines, and (7) by such minor methods as spraying, close pasturing of Ribes, and the removal of the diseased plants or parts of them.

QUARANTINE.

In North America (131, p. 54–55), Canada took the first official action against the white-pine blister rust, placing it on her list of proscribed plant diseases and later prohibiting the entry of all 5-leaved pines from all other countries. Since then (2) a quarantine has been declared against the shipment of Ribes from points east of a line between Saskatchewan and Alberta to points west of that line. The shipment of Ribes to points west of this line is allowed from points in the United States south of the above protected area. These modifications are made to help protect the western white-pine area from the shipment of this disease in nursery stock, and to connect with the Mississippi Valley quarantine line in the United States, which has been established with this end in view (fig. 13). The United States Government in 1912 (94) put in force a regulatory act controlling the entry and movement of nursery stock. This act prohibits the entry of 5-leaved pines and of Ribes from Europe, Asia, and Canada; forbids the shipment of such stock from the eastern section of the country to points west of the western boundaries of the States of Minnesota, Iowa, Missouri, Arkansas, and Louisiana; and also forbids the

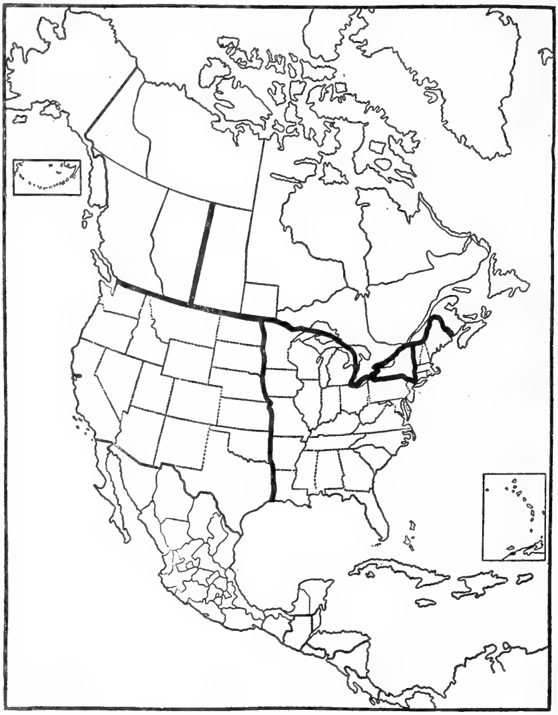

FIG. 13.—Outline map of North America, showing the quarantine lines established by the United States Department of Agriculture to control the white-pine blister rust by prohibiting the shipment of the host plants from infected territory to uninfected sections. The quarantine line established by Canada to prevent the shipment of diseased nursery stock across the prairie region from the eastern Provinces is also shown.

shipment of 5-leaved pines and of *Ribes nigrum* from the States of New England to any of the other States and from New York to points outside that State. Still more recently, an absolute embargo has been placed on ornamental and forest tree and shrub stock from other countries (fig. 13).

These quarantines prevent our getting more of the white-pine blister rust from other countries. The Great Plains region forms a natural barrier (fig. 13) against the spread of this disease from the East to the West (97, 98, 141, p. 7; 148)). Since it is already well distributed and established east of this barrier, the immensely valuable western white pines can be protected very efficiently by preventing the shipment of white pines and Ribes from the infected section to the western region, which is still free from the disease. This is accomplished by quarantine, which is designed to prevent the shipment of infected stock from a generally infected district to those States which are not generally infected and to exclude plant pests from all the rest of the world (98).

Within the past four years many of the various States have enforced regulatory measures with reference to this disease (94). These States are California, Delaware, Georgia, Idaho, Illinois, Indiana, Kansas, Maine, Maryland, Massachusetts, Michigan, Minnesota, Montana, Nevada, New Hampshire, New Jersey, New York, North Carolina, Oregon, Pennsylvania, Rhode Island, South Carolina, South Dakota, Tennessee, Vermont, Washington, West Virginia, and Wisconsin.

ERADICATION OF ADVANCE INFECTIONS.

In 1909, when *Cronartium ribicola* was first found upon white pines in North America, it appeared to occur only on recent shipments of young trees from Europe. That is, it was present in advance infections, and so far as could be determined there was no generally infected area. Since that time areas have been found which are generally infected, and we have both types of infections to reckon with. (See figs. 2 to 12.) Where advance infections were small it appeared to be feasible to attempt eradication of the disease, but when generally infected areas were found eradication became impossible, and local control was the only feasible thing to be attempted.

When this disease was first discovered on Ribes in 1906 at the Agricultural Experiment Station at Geneva, N. Y., an attempt was very properly made to eradicate the disease. All of the Ribes in the infected plat were destroyed. Very few white pines were within half a mile, and none of these were found diseased. Stewart (150) published an excellent account of this case. It was not then known that the æciospores readily blow for miles in a viable condition, nor was that fact established until rather recently (128, 145, 146).

In 1909 it was learned that great quantities of infected young white pines had been imported from Europe in 1907, 1908, and 1909. (Fig. 1.) With conditions as they appeared to be, it was believed that eradication might be possible, and this was attempted. The disease was held in check in such shipments of diseased trees as could be located. But many could not be located. Moreover, for years before, as was subsequently learned, nurserymen and private individuals had imported from Europe many infected white pines. These we had no means of knowing about until too late, since the importers and planters did not inform us concerning them, even after the publication of warnings against the disease. Such diseased importations have been the center s from which most of our large outbreaks have started. So far as we can learn no Federal agency has imported white pines upon which this disease has been found.

More complete knowledge of the life history of the fungus has shown that it is impossible to eradicate it where both Ribes and white pines are native and abundant, after the æciospores are once set free in quantity. If both pines and Ribes be removed from a given area the disease may be eradicated in that area but it will have escaped beyond that area by means of the æciospores. This happened in Minnesota and Wisconsin, where all the white pines and Ribes were removed from large infected areas.

The removal of pines has been accomplished in a few cases. Entire plantings of imported pine stock were destroyed soon after they were found to be diseased, and in these cases Ribes were also removed or were absent from the area treated. The forestry officials of the State of New York took the lead in this work, destroying 1,200,000 imported trees in their nurseries in 1910 and 1911. A number of plantations were also destroyed in New York, New Jersey, and Vermont (131, 139). As early as 1912, the total destruction of diseased lots of imported white pines (133) was urged rather than weeding out only those which were visibly diseased. Public opinion would not permit this to be done in the wholesale manner that was necessary for efficiency. Yet this was the one efficient manner of handling such imported trees (136) before generally infected areas had developed.

SEPARATION OF THE TWO HOSTS.

The fact that each form of spore will infect but one of the hosts, at once indicates that a separation of these hosts will prevent the further progress of the parasite within the control area. If the pines only are removed, the disease will be likely to die out on the Ribes, since it apparently overwinters on them only infrequently; if the Ribes are removed, the disease is isolated on that particular lot of pines, where it overwinters (if the diseased trees are not also found and removed) and produces new crops of æciospores each spring. The disease is kept from attacking more pines within the area where the Ribes are removed, but it may spread to Ribes miles away, there to start new pine infections, each of which will act as a new center of infection in future years. This makes it practically impossible where both white pines and Ribes are native entirely to eradicate the disease after the æciospores are once set free.

REMOVAL OF PINES.

In all work where pines have been removed the Ribes have been absent or were also removed; hence, all this work is placed under "Eradication of advance infections." In some of the States, Ribes-growing sections are being established, and it is expected that white pines will be entirely removed from such areas.

REMOVAL OF RIBES.

Experiments on a large scale are in progress in all of the States of New England and in New York, Wisconsin, and Minnesota for the removal of all Ribes in certain areas, to determine whether it is practicable thus to protect valuable white-pine stands.

Much work of this sort has been carried on during the past four years. Infected areas have been chosen and the Ribes removed under various conditions to show what possibilities there are in such work (23, 24, 25, 103, 104). The removal of all Ribes plants in a given area is a difficult matter. Wild Ribes offer the greatest difficulties. It is not humanly possible to find every plant in wild woodland; plants pulled up, if left touching the soil, may again take root and persist in a living condition; pieces of root crown and occasional pieces of roots left in the soil sprout and make new plants (23, p. 8); fruits on the pulled bushes fall off and start a crop of seedlings to replace the parent plant; seeds of old fruits already on the ground may germinate and start seedlings. Nevertheless, the results of this work are encouraging. Wild currants and gooseberries do not reproduce rapidly in an area that has been worked by an efficient crew. Thorough checking on 2,485 acres in 8 separate tracts previously gone over by eradication crews showed that on an average acre, 62 bushes (95.5 per cent) were destroyed in the first working and 3 bushes in the second working. Of the latter, two bushes were missed in the first working and one bush developed from seeds or sprouts. The remaining plants are so small that they carry but 1 to 2 per cent of the total Ribes leafage (24). Moreover, they are usually so low or so covered with other vegetation that very few become infected, so that the work results in almost perfect control of the disease. To judge from data at hand, control areas usually should be reworked within 10 years after the first working (25).

Two principal methods of removing Ribes have been developed. Where Ribes are abundant the Ribes eradication crew has to cover all the ground and pull the Ribes as they go. Where Ribes are relatively scarce they are likely to occur only in certain favorable locations. In such territory an expert scout covers the ground, mapping it and indicating the Ribes areas to be worked by the crew. In favorable localities this has proved successful and greatly reduces the cost of Ribes eradication (25). Experiments in the killing of thick stands of wild Ribes with chemicals indicate that this method (113) materially reduces the cost.

Ribes eradication was started as early as 1909, but at that time was limited to plantations of infected imported white pines and to a safety belt of 100 yards around them. In 1910, the width of the safety belt was increased in some of the States to 500 feet, and in 1915 in Massachusetts to 500 yards. In 1916, 600 yards was taken as the safe width for all situations. Prior to 1919, facts concerning the spread of *Cronartium ribicola* from Ribes to pines were not definitely known. As a result of the investigations of the germination and dissemination of the sporidia the width of the Ribes-free zone was set, in 1919, at 200 to 300 yards for average conditions (25, 146).

In 1917, when extensive areas were first cleared of all Ribes, lack of experience in such work by all connected with the work greatly reduced its efficiency, but even then it was found that the outlook was not hopeless, although the cost of eradication of Ribes was too high to be justified except where pine stands were valuable. Efficiency has been steadily increased since then until it has been found that men green in this work can be quickly taught to find and destroy at least 95 per cent of all wild Ribes plants the first time over the ground (24, 25). A system of checking the work has been developed, as well as a system of accounts, so that present results are quite accurately known.

The cost of Ribes eradication has been steadily reduced. In 1918, 105,977 acres were worked in New England at a labor cost of 44 cents per acre. In New England and New York the average cost per acre including supervision in 1918, was 66 cents. In 1919, in New York and New England, 252,114 acres were worked at an average cost per acre of 54 cents, including supervision, and of 42 cents for actual labor (24, 25). Improved methods are expected to reduce still further this cost as, in New England alone, the cost in 1919 was 24 cents per acre, owing to the use of improved methods (24).

The efficiency of Ribes eradication with respect to pine infection will become evident as time elapses. Examination of areas where Ribes were eradicated in 1916 and 1917 has shown no new pine infections. This is in spite of the considerable number of Ribes missed in the early work.

The experiments in the removal of Ribes on an extensive scale have gone far enough to prove that it is a practical method of protecting pine stands. Accordingly the public has been urged to destroy wild and cultivated Ribes within at least 200 yards of valuable pine stands in the generally infected regions.

Assistance to individual pine owners, towns, and associations in protecting pine areas from the blister rust is given by the New England States, New York, Wisconsin, and Minnesota, in cooperation with the United States Department of Agriculture. In 1919, about $10,000 was subscribed for cooperative eradication of currants and gooseberries by individuals and associations in New York. In Massachusetts, local cooperators furnished $1,075. In New Hampshire, 53 towns voted appropriations totaling $8,514, and 34 individuals and firms subscribed $2,053 additional. The interest of the public in blister-rust control is further evidenced by the fact that this State destroyed 21,171 bushes of cultivated currants and gooseberries belonging to 1,023 owners, and only 3 owners insisted on compensation for their bushes (24).

The State and Federal authorities favor cooperation with towns, counties, associations, or groups of individuals in order to free from Ribes as large an area as possible in each locality. This reduces cost per acre and increases the effectiveness of the protection to pines.

SCREENING RIBES AND PINES WITH OTHER SPECIES.

Screens of heavy underbrush or trees surrounding or covering Ribes will do much to prevent infection of the Ribes by æciospores and will greatly reduce infection of white pines, if the Ribes do become infected (145, 146).

Screens or windbreaks of other kinds of trees around the edge of white-pine stands will greatly reduce infection on the pines. In the same way, planting in mixture or in strips alternating with another species should help to keep the disease down.

SELECTION OF SITES FOR PINES.

Infection by *Cronartium ribicola* may be reduced to a minimum in a generally infected area by judiciously choosing a site for the planting or natural seeding of white pines. Areas where there is a minimum number of Ribes, or where they have been eradicated, which are not in moist locations and are not especially subject to fogs or mists, and which are protected by forests or conformations of the land from heavy sweeping winds, are favorable for the encouragement of the growth of white pines. The converse conditions are to be avoided as far as possible.

SPRAYING.

Spraying has been little used in North America to control the white-pine blister rust, as the chances for success have appeared to be slight. Spraying of Ribes to prevent their infection has been tested in a number of instances.

In 1915, McCubbin (86) carried on some careful spraying tests with *Ribes nigrum* plants, using both Bordeaux mixture and soluble sulphur in parallel experiments. The following statement has reference to spraying that was done every two weeks through the summer:

> It was realized that the spray would have to be applied to the under sides of the leaves to be effective, and though this was done as thoroughly as possible in our work, it must be admitted that it takes so much time and care that satisfactory spraying of this kind would be out of the question in a commercial way. Owing to frequent rains during the summer, the best results were not obtained from this work, but even allowing for this it was certain that, though the rust can be greatly reduced by spraying, it can not be controlled sufficiently to prevent the spread of infection. Consequently, whatever value spraying methods may have as a means of protecting individual plantations, they are likely to be of little use in combating the disease as a national pest. In this connection, it has been suggested by the Dominion Botanist that since spraying will not completely control the rust, it may work a positive harm by keeping the infected leaves longer on the bushes in the fall, and thus materially extend the period during which infection of the pine may take place, providing, of course, that the infection of pines is possible throughout the whole season.

Stoddard, in 1918 (23), carried out a spraying test in Connecticut, with the following results:

> Spraying experiments for the control of the blister rust were conducted on red and black currants. Results were nearly negative on red currants because of lack of infection. On black currants spraying gave nearly complete control throughout the season. However, such careful and frequent spraying had to be done that it is not considered to be a practical method of control.

No experiments have been made in the spraying of pines, as it has appeared useless in larger trees where the infections have occurred. Seedlings in seed beds of nurseries may perhaps be protected from infection by spraying, as has been suggested by Clinton and McCormick (14). It should be well tested under extreme conditions (106).

CLOSE PASTURING OF RIBES.

The use of animals to feed on the leaves of Ribes is feasible if the area is pastured heavily until well cleaned up. Sheep are very close feeders and undoubtedly can be thus utilized (23, p. 7). Goats are the most promising animals for the purpose, however, as they are omnivorous feeders. This method can be recommended only for areas where small pines are absent or too few to be of value.

REMOVAL OF DISEASED PARTS AND DISEASED PLANTS OF RIBES.

The removal of the infected leaves has been attempted in a few lots of *Ribes nigrum* in nurseries, but it is costly and merely palliative in that it is usually only postponing more drastic measures. The cutting back of infected Ribes bushes has been tested in a few instances, but like the plucking of the leaves, it is usually unsatisfactory, since the bush remains to take infection another season.

The removal of diseased plants only of Ribes is unsatisfactory, as it has been found that it requires repeated visits through the season for the removal of plants which have developed the disease since previous inspections. This makes the cost of the work prohibitive, and the disease progresses in spite of it.

REMOVAL OF DISEASED PARTS AND DISEASED PLANTS OF PINES.

The removal of diseased parts of infected pines does not appear to be an economical procedure from the viewpoint of the lumberman or wood-lot owner, because of the low value of single trees. For highly valued ornamental trees it becomes possible financially. Under such conditions, the removal of all Ribes to prevent new infecton, accompanied by careful cutting out of all infections in the pines for several years, will finally result in the elimination of the disease from those trees. Martin, Gravatt, and Posey[58] have investigated the possibilities of this type of work. They conclude that—

> Experimental and practical results show that ornamental pines which have already become diseased can be saved by cutting out the infected parts if treatment is applied in time. The work is easily performed at a comparatively low cost. Treatment can be given any time during the year, but best results will be obtained from April to June when the cankers are more easily found because of the bright orange-yellow blisters. Successful treatment depends primarily upon ability to find the cankers and determine accurately the edge of the diseased area. The workmen should be thoroughly familiar with the symptoms and appearance of the disease on pines.

Where the Ribes can not be thus eradicated, other species of trees should be planted to take the place of the white pines. Cutting out infections depends, for success, on finding all of them. The workman must be familiar with the blister rust and be thorough or the results will not justify the cost. If a tree is nearly girdled near the ground, or if most of the branches must be removed, it is useless to attempt to save it. The cutting out must be repeated for several years after all the Ribes are eradicated, as dormant and slightly developed infections become visible. Cutting out experiments showed that cutting back for 1½ inches or more from the extreme edge of the infected area insured removal of all diseased bark and stopped the disease in those areas. In practice this distance should be increased to 5 or 6 inches to insure thorough work.

On a main trunk an infection which has extended only part way around the trunk may be treated by peeling off the bark on the canker and to the required distance around it. In this case the safety zone should extend for 4 or 5 inches directly above and below the diseased area but need not extend more than half as far sidewise.

The removal of only diseased white pines in infected imported trees has been inefficient and costly, even where the Ribes were removed too. Records of such work in about 900,000 imported trees (136) shows that it is inefficient, although the disease has been checked somewhat. The cost has been great enough to have replaced the imported trees with healthy home-grown ones.

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[58] Martin, J. F., Gravatt, G. F., and Posey, G. B. Treatment of ornamental white pines infected with blister rust. U. S. Dept. Agr. Cir. 177, 20 p., 12 fig. 1921. Seen in manuscript.

In a region where Ribes are rare or practically absent the removal of the diseased pines only may serve to prevent progress of the disease. This allows the dispersal of æciospores and may result in scattering infection on Ribes miles away. In such cases it will take a long time to detect the escape of the fungus. In areas free from the Ribes the aim should be eradication rather than control of the disease, as such areas are the very ones where white pines should be grown in the future.

In generally infected districts where Ribes are removed for some distance, it may pay to cut out the worst infected trees to reduce the crop of æciospores and thus reduce infection around the borders of the treated area.

Status of the Control of White-Pine Blister Rust.

The present status of the control of the white-pine blister rust in North America may be summed up as follows:

> Eradication of *Cronartium ribicola* is impossible except in small, isolated, advance infections. It should be attempted only in localities where the disease is quite limited in distribution and well separated from the known generally infected areas shown in figure 2. As a national problem, control is the only feasible thing. Protection of uninfected or sparsely infected areas by enforcement of the present Federal quarantines is necessary, since this disease is distributed to great distances only by means of infected nursery stock. The western forests of white pines can be protected from the blister rust for an indefinite period by rigid enforcement of the Mississippi Valley quarantine. A single diseased shipment may undo all attempts to restrict it to the eastern forests.

In the eastern forests blister-rust infection on *Pinus strobus* is rapidly developing. A strip survey in one locality in New Hampshire (24) shows that one-fourth of the white pines on an area of 72 square miles are now infected. The areas marked as generally infected in figure 2 show the great increase in general pine infection. Much of this infection will become visible in the next three years. It is an insidious disease, a tree not being noticed as diseased until it is heavily infected. There is abundant evidence that it is destructive to merchantable trees as well as to younger ones. It is just getting under headway.

Ribes nigrum is far the most dangerous species, but all Ribes are dangerous to white pines in generally infected areas. In such areas the disease can be controlled by the removal of all Ribes. Local control depends on the removal of Ribes within white-pine areas and the education of the white-pine owners to remove Ribes as a routine part of white-pine forest management. Local control by the removal of Ribes can be taken up at any time in the future, but if the present stand of trees is to be saved action must be taken at once.

A few years delay will mean serious loss. It is a simple and practical precaution to destroy the currant and gooseberry bushes before they destroy the pines. The demonstrated effectiveness of this method of control justifies pine owners in uprooting currant and gooseberry bushes on a large scale (24).

Those who do not do this in their pine lands and for a distance of 200 to 300 yards outside will be likely to see a valuable asset turned into a liability. In areas where the white pine is an important tree cultivated Ribes should not be planted. A number of States already have laws prohibiting such planting without permission from the State authorities except in areas designated and set apart as "currant-growing districts."

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